Population ecology of landlocked Arctic charr, *Salvelinus alpinus L.*, in the Canadian High Arctic

Thesis

Population Ecology of Landlocked Arctic Charr, *Salvelinus alpinus L.*, in the Canadian High Arctic

Henry Hardyman Parker

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To my friends and colleagues in submarines.

Abstract

The thesis describes fieldwork conducted during the Joint Services Expeditions to Ellesmere Island 1988, 1991 and subsequent modelling activities. Four landlocked populations of Arctic charr, *Salvelinus alpinus* L., were surveyed at 81 °N, close to the northerly extreme of the species range. They were single-species populations consisting of two distinct size modes, "Dwarf" and "Normal" charr, but with major differences both in size and relative numbers between the lakes. Tentative correlations between population structure, growth rate variation and possible genetic divergence are suggested by this fieldwork and the models examine their credibility. The key hypothesis is that the alternative life history strategies represented by Dwarf and Normal charr represent different solutions to the problem of energy limitation within a size-structured population. Major findings of the models are that alternative life history strategies should be expected to be optimised at different growth rates; density dependence implies that Dwarfs and Normals have equal fitness; a high average juvenile growth rate is likely to lead to a large number of Normals relative to Dwarfs; and that maximum individual fitness is probably achieved in bimodal populations within a "semi-speciated" condition. A combination of evidence further suggests that cannibalism is a likely mechanism for maintenance of the bimodal population structures; and the form of a reaction norm for choice of life history strategy is predicted and found to be similar to one experimentally determined for smolting in Atlantic salmon, *Salmo salar* L..

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Enclosures

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5. Correspondence from Dr. PATALAS (Zooplankton)
6. Parker, H.H. & Johnson, L. (1991).

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Acknowledgements

As a part time project, this thesis has taken eight years to come to fruition from its unofficial inception in 1987. I have received assistance from many in my private life, in the scientific community, and in my full-time profession. I cannot possibly acknowledge everybody and apologise to those whom I may have inadvertently left out.

I owe a special debt to my Director of Studies at British Antarctic Survey, Dr. Cynan Ellis-Evans. He has given much of his own time to guide me through the administration of this project; and has provided encouragement and general scientific guidance throughout.

The breadth of the subject matter has also made it essential that assistance was sought from a significant number of other people since no one person could cover the whole project. Generally scientific collaboration was arranged on a personal rather than official basis and was at two levels. At the higher level, it effectively resulted in supervision albeit usually at some considerable arm's length and I have taken the unusual step of acknowledging each supervisor in the relevant chapters. They are:-

Dr. Lionel Johnson	Arctic charr	Department of Fisheries and Oceans, Winnipeg, CANADA
Professor Clive Kennedy	Parasites	University of Exeter, UK
Professor Roger Nisbet	Modelling	University of California, Santa Barbara, USA

At the lower level, assistance was obtained to provide a specialised data input to the overall ecological picture. In these cases, I conducted the fieldwork and provided samples but thereafter my involvement ceased. This assistance is included in its original form as enclosures. Relevant people are:-

Dr. Cynan Ellis-Evans	Limnology	British Antarctic Survey, UK
Dr. Peter Langton	Insects	11 Felix Rd., Ramsey Forty Foot, Huntingdon, UK
Dr. Oyvind Schnell	Insects	Bergen University, NORWAY
Dr. Kaz Patalas	Zooplankton	Department of Fisheries and Oceans, Winnipeg, CANADA

I would also wish to acknowledge the contribution of the full-time students who have provided a broadening perspective during my periods in full-time academia. I would particularly wish to mention Doug Donalson from Santa Barbara who tolerated my invasion of his office for six months in 1994, but there are others who had a profound influence over shorter timescales. In a similar vein, I want to thank the professional participants of three conferences who patiently explained the issues and updated me on the genetic work which is beyond the resources of the individual to conduct.

The project would not have been possible without the logistical flair and drive of Flight Lieutenant Bill Hankinson, Royal Air Force, who organised the two Joint Services Expeditions to Borup Fjord 1988, 1991. I was also willingly assisted by Bruce Crawford and Dr. Kate Silvester in the field, as well as having more occasional help from other members of the team.

Financial assistance in the form of grants to the expedition was received from a number of sources including the British Ecological Society and Services non-public charities. I am grateful to the Institution of Electrical Engineers for paying for my attendance at a conference in Alaska.

Finally, I would wish to thank my family for their support and the many friends, especially in the Royal Navy, who have allowed me to indulge my fascination. It has been a great experience, but one in which sacrifices have been made. For those who have involuntarily shared that sacrifice with me; I regret that I have occasionally been irritable, irrational and intransigent. In retrospect, I hope you can hear the laughter and the vibrancy of the clear, cold Arctic summer; and the myriad mysteries and miracles which belie the desolation of a last great wilderness.

Declaration

I hereby declare that the research reported in this thesis was carried out by myself and that the thesis is my own composition. The contribution and technical assistance of colleagues is acknowledged.

The work on this thesis was performed whilst employed by the Royal Navy and registered as a candidate for the degree of Doctor of Philosophy with the Council for National Academic Awards, later transferred to the Open University. None of the material presented in this thesis has been submitted for any other award.

1. Introduction

1.1 The Arctic - an Extreme Environment

There is no universally accepted definition of what constitutes the Arctic; each has its advantages depending on the research topic of interest. For the purposes of terrestrial and freshwater ecosystems, perhaps the best is that of Köppen (1900) who defines a polar climate as one in which the mean temperature of the warmest month does not exceed 10 °C. The associated isotherm correlates roughly with the treeline which is less precise since it can seldom be sharply defined. (Sage 1986).

Key features of the Arctic climate are that it is cold, windy, dry and extremely seasonal. This is reflected in the collection of basic statistics from Eureka, Northwest Territories, Canada (80°00' N, 85°56' W) presented at Table 1.1. The fundamental climatological driving force is solar radiation. As latitude increases, the angle of incidence of this radiation decreases thus reducing its intensity, but this is compensated for, to some extent, by increasing daylength (for example, a continuous polar day of 3½ months duration at 75 °N). The high reflectivity (or albedo) of snow also considerably reduces the amount of solar radiation which is absorbed. Overall, increasing latitude correlates with a greater proportion of annual radiation being required to melt the snow as opposed to its acting as the primary source of energy to the Arctic food web. In some parts of the Arctic the growing season may be as little as 40 days. (Sage 1986).

Month	Mean sta. press. (mbar)	Mean daily temp. (°C)	Mean daily temp. range. (°C)	Temp. extr. (°C) highest	lowest	Mean precip. (mm)	Max. precip. in 24h (mm)	Mean snow-fall (mm)
Jan	1016.6	-35.9	6.4	-1.1	-51.1	3.1	3.1	30.5
Feb	1017.1	-37.3	5.8	-12.2	-52.2	1.8	3.6	17.8
Mar	1023.3	-37.6	5.9	-13.3	-52.8	1.5	5.1	15.2
Apr	1022.0	-26.8	7.8	-3.3	-45.6	1.8	3.8	17.8
May	1019.6	-9.7	6.3	5.6	-31.1	2.8	5.6	27.9
Jun	1014.4	2.7	4.8	17.8	-13.3	3.3	14.5	7.6
Jul	1009.2	5.7	5.6	19.4	-2.2	15.5	13.0	7.6
Aug	1012.0	3.8	4.5	15.0	-8.3	13.5	41.7	15.2
Sep	1012.9	-6.7	4.4	5.6	-26.1	10.9	13.7	106.7
Oct	1011.3	-21.6	6.6	3.9	-41.7	8.9	13.5	88.9
Nov	1014.9	-30.6	6.6	-1.7	-44.4	2.0	1.5	20.3
Dec	1013.5	-35.2	5.7	-10.6	-49.4	2.0	2.5	20.3
Annual	1015.6	-19.1	5.9	19.4	-52.8	67.1	41.7	375.8

Table 1.1 Climatic table for Eureka (80°00' N, 85°56' W, elevation 2.4 m). Data based on records 1951-1960. From Orvig 1970.

The main effects of climate on the biology of the Arctic are that species diversity and rates of production are low. Only 48 species of land mammal occur in the Arctic of which only 9 extend to the Canadian Archipelago. This compares with a world total of about 4,000. (Sage 1986). Similarly, various types of closely-related charr are the only freshwater fish to survive at the extremes of northerly latitude.

In addition to the constraints imposed by long-term climatic averages, Arctic wildlife must contend with unpredictable and violent weather. The difference in maximum and minimum monthly temperatures in Table 1.1 serves to illustrate one aspect of this point; and the weather typical of early and late summer routinely wreaks havoc on some Arctic populations. In the autumn of 1973, for example, an October rainstorm created a layer of ground ice that muskoxen could not break through to feed. Nearly 75% of the muskox of the Canadian Archipelago perished that winter. This is just one of many cases which cause the biologist to label these arctic ecosystems as "stressed" or "accident-prone". (Lopez 1986)

Comparison between the terrestrial climate and lake microclimates reveals some differences. Lakes have a high degree of thermal capacitance which buffers them against environmental fluctuation. There is, nevertheless, some measure of fluctuation since, for example, Lake Hazen on Ellesmere Island, Canada, becomes ice-free only in some years (Sage 1986). A related effect is that of thermal lag, with large lakes reaching their maximum temperatures later in the year than small ones.

Contrasts between land and lake are apparent through biological as well as physical manifestations. Terrestrial populations of mammals, for example, are famous for their cyclic nature; the best known being the lemming, and snowshoe hare-lynx, systems (Sage 1986). This compares with good evidence that charr systems hardly fluctuate at all (Johnson 1994). At an individual rather than population level, terrestrial mammals, insects and plants all exhibit marked degrees of behavioural and physiological adaptation to their environment. This is not apparent with fish. Migration, for example, is one adaptation unavailable to landlocked fish. Similarly, there seems little physiological difference between an Arctic charr from Ellesmere Island (81 °N) and one from a temperate lake such as Lake Geneva (46 °N).

Arctic land ecosystems are well known for their simplicity and lake systems are equally simple. Some of the simplest biological systems outside of the laboratory are in these practically closed landlocked lakes with only one fish species; and they are thus an especially suitable subject for modelling studies. To quote Lopez (1986) however, "this sensation of simplicity would be something of an illusion. Arctic ecosystems have the same elegant and Byzantine complexities, the same wild grace, as tropical ecosystems; there are simply fewer moving parts... . The complexities in Arctic ecosystems lie not with, say, some esoteric dietary preferences among 100 different kinds of ground beetle making a living on the same tropical acre, but with an intricacy of rhythmic response to extreme ranges of light and temperature. ... . And with their adaptation to violent, but natural fluctuations in their population levels."

1.2 The Joint Services Expeditions to Borup Fjord

The fieldwork described in this thesis was conducted as part of two Joint Services Expeditions to Borup Fjord, Ellesmere Island, in 1988 and 1991 (Figure 1.1). The main aim of the expeditions was to survey the biology of what was, at the time, a largely unexplored area of the Arctic. The teams consisted of both Servicemen and civilian scientists, with the intention of combining the logistic expertise of the Services with the professional scientific facilities available at a number of academic institutions in UK and Canada.

The expeditions were in the field from 12 May until 24 August in 1988, and from 22 June to 9 August in 1991. Travel was largely by traditional means; by ski, foot and boat. Despite this logistic limitation, a total of nearly six months of fieldwork was achieved at the extreme North of the Arctic charr's distribution. This is well in excess of the brief surveys previously conducted at these latitudes and represents the most northerly investigation of landlocked Arctic charr populations to date.

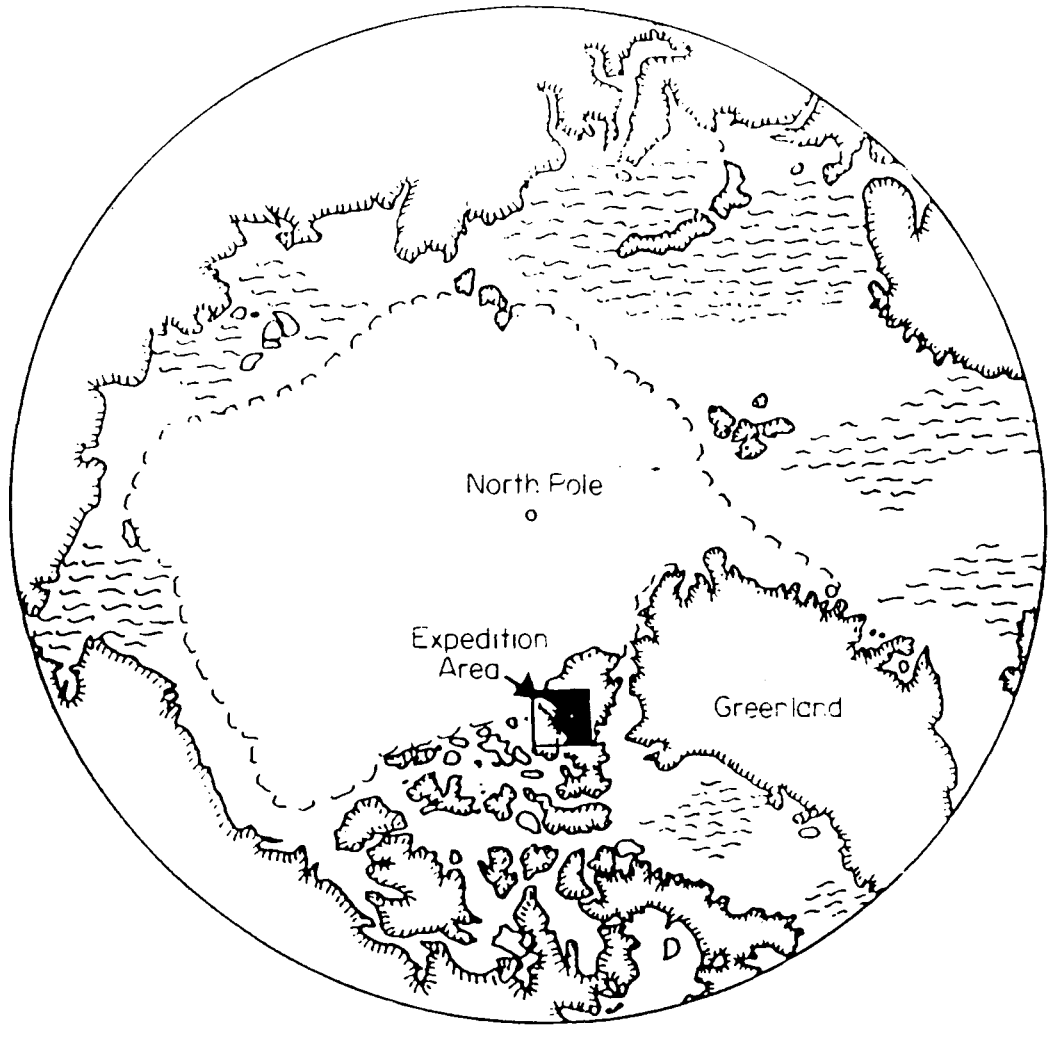


Figure 1.1 Map showing location of Borup Fjord, Ellesmere Island and the study area. Lake H is at the head of Essayoo Bay and Lakes A, B and C are in Midnight Sun Valley at the head of Oobloyah Bay.

1.3 Study Area

The study area comprised the Essayoo and Midnight Sun Valleys opening respectively onto Essayoo and Oobloyah Bays at the head of Borup Fjord. Essayoo Valley contains a relatively large unnamed lake (referred to as Lake H) which was the major preoccupation of the study. Midnight Sun Valley contains several smaller lakes (Lakes A, B, and C in order of declining altitude) (Figure 1.1). The sparse vegetation of these valleys is tundra heath with patches of bare rock. Flow in the streams is greatest over the period of snow-melt in June, but declines to virtually nothing after the thaw.

According to Hankinson (1990):-

"The terrain of Borup Fjord is mountainous with deep fjords and large valleys dominated by braided rivers fed by glacier melt-water during the thaw. The landscape was formed by sedimentary succession ranging from carboniferous to early Tertiary; igneous activity probably took place during late Cretaceous and the area was uplifted, folded and faulted during the Eurekan Erogeny (40 m. yrs. B.P.). More recently, the area was probably glaciated during the Quaternary and strong glaciation during the early Wisconsinian is possible but this can not be proved. It is however possible that parts of the area remained ice free even at the peak, 18-20,000 yrs. B.P., of the Wisconsinian glaciation. The valley plains were probably formed around 7,000 yrs. B.P. (Barsch & King 1981) while the glaciers are probably still close to their maximum extent following the climatic depression that ended around 1925."

"Borup Fjord and the surrounding seas are frozen for most of the year; although Essayoo and Oobloyah Bays appear to clear reliably every year, due to the influx of warmer water from the rivers, there are many years when Greely Fjord, at the mouth of Essayoo and Oobloyah Bays, does not open up. Climatically there is evidence that it falls between the continental and maritime zones of Ellesmere Island but it shows more continental features than the nearby (80 miles) weather station at Eureka. This favourable climate produces a diverse and, by Ellesmere Island standards, prolific flora that supports substantial numbers of birds and mammals."

1.4 Description of Study Lakes

Supervised by Dr. Cynan Ellis-Evans

The only fish species present in the four study lakes was the non-migratory form of Arctic charr. The populations in each lake were completely isolated from each other and from the ocean (i.e. ' landlocked '). In the short open water season the interchange of organisms between the lake and the external world was limited, consisting of emerging aquatic insects and some predation on the fish stock by birds such as divers, *Gavia* sp., and Arctic terns, *Sterna paradiseaea* Pontoppidan. Other lakes in Midnight Sun Valley were examined for charr using gillnets but with no success. In these lakes the fairy shrimp, *Epidurus* sp., was abundant and it is thought they were too shallow to support a fish stock under the ice in winter. It is estimated that ice covers the lakes for approximately 10 months each year.

The study lakes are ultraoligotrophic and their general features are summarised at Table 1.2. All lakes exhibited low conductivity, indicating poorly-buffered waters of low ionic content. The lower conductivities of Lakes A, B and C may reflect their greater distance from the sea. They were all somewhat alkaline. Water derived from snowmelt and precipitation was the only source of inflow, and the large braided rivers carrying glacial meltwater bypassed the lakes in both valleys

Lake	Position	Altitude (m)	Catchment Area (ha)	Surface Area (ha)	Depth (m)	Bottom Type	pH	Conductivity (μS cm^{-1})
A	80°54'00" N 82°11'15" W	250	c.5	4	12	Small stones	8.45	70
B	80°53'30" N 82°17'08" W	215	c.25	4	9	Silt/ large stones	8.45	61
C	80°51'00" N 82°59'00" W	105	c.300	4	>5	Silt/ marginal vegetation	8.18	94
H	80°51'00" N 82°52'00" W	30	c.600	75	15	Glacial silt	8.00	200

Table 1.2 Location, altitude, catchment area, depth, bottom type, pH and conductivity of Lakes A, B, C and H. Data from August 1988.

Information on the physical characteristics of the water column in all four lakes was also obtained. Sampling of water from different water depths was achieved by IOS bottle or diaphragm pump. Temperature, conductivity, dissolved oxygen and pH were measured using appropriate probes.[1] Alkalinity was measured for Lake H in 1988 by titration against hydrochloric acid and, combined with temperature and pH data, this was used to calculate total carbon dioxide (Mackereth *et al.* 1989).

The limnological data obtained in 1988 and 1991 differed in a number of important respects. The equipment used in 1988 allowed less accuracy and fewer data points. On the other hand, the 1988 field season was longer; and the weather calmer meaning that mixing processes driven by wind were less significant.

1.4.1 Lake H

The limnological data for Lake H in 1988 and 1991 are presented in Figures 1.2 and 1.3 respectively. Different graphical formats are used to highlight different aspects of the data. Prior to the thaw, the water column was stable with conductivity increasing with depth and temperature increasing from 0.7 °C immediately beneath the ice canopy to 2.6 °C at the bottom (18 May 1988). As the ice began to melt, water of low conductivity appeared beneath the ice. This is purely due to ice melt and not inflow effects since the

[1] 1988 - pH meter - Philips PW9624 # 119320
- Conductivity meter - Philips PW9529 # 119302
- Temperature/ Dissolved Oxygen meter - Jenway 9070 # 16899

1991 - pH meter - Jenway 3070 # 36224
- Conductivity meter - HI 8033 # 25976
- Temperature/ Dissolved Oxygen meter - YSI Model 57 #6926

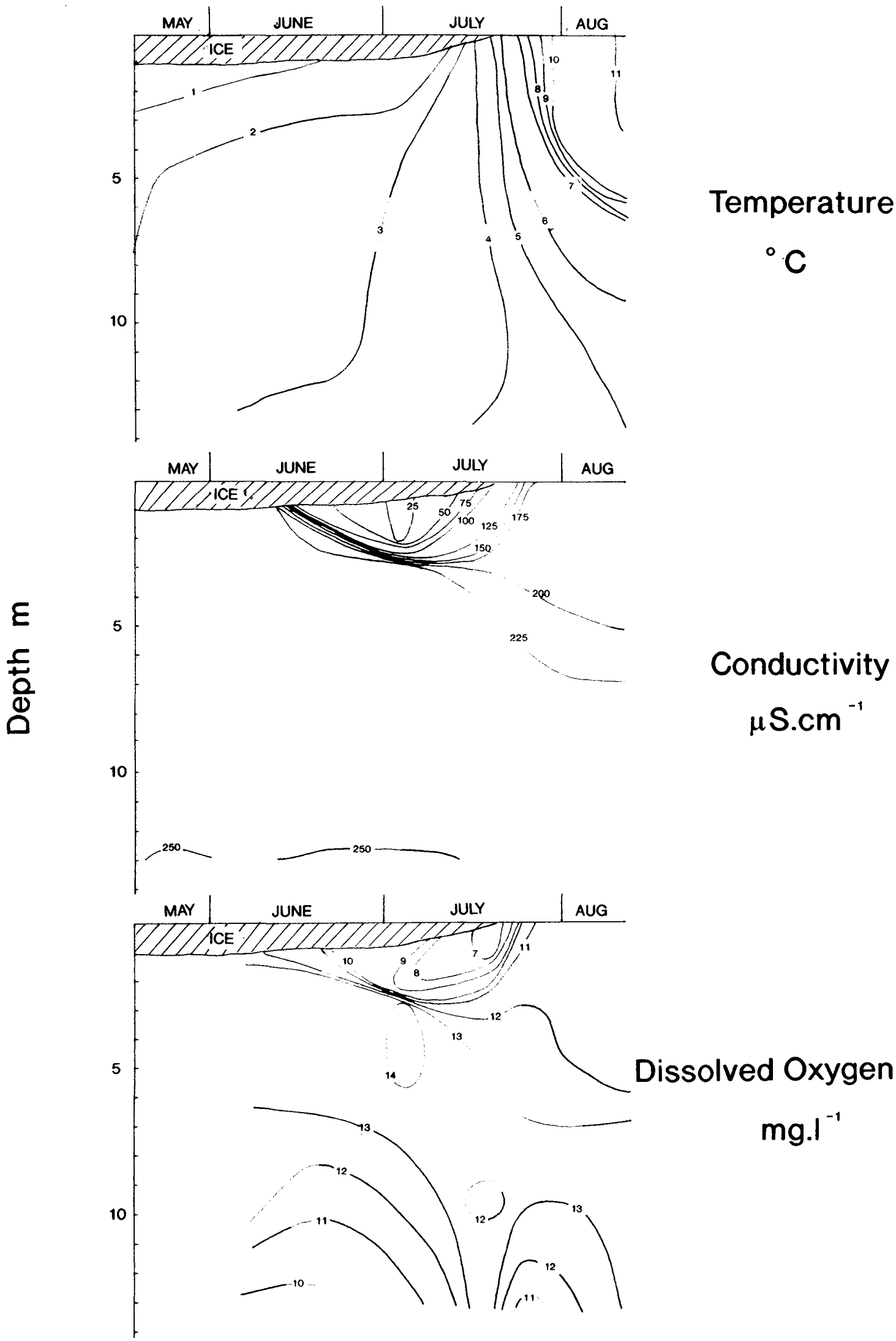


Figure 1.2 Isopleths of limnological data from Lake H in 1988.

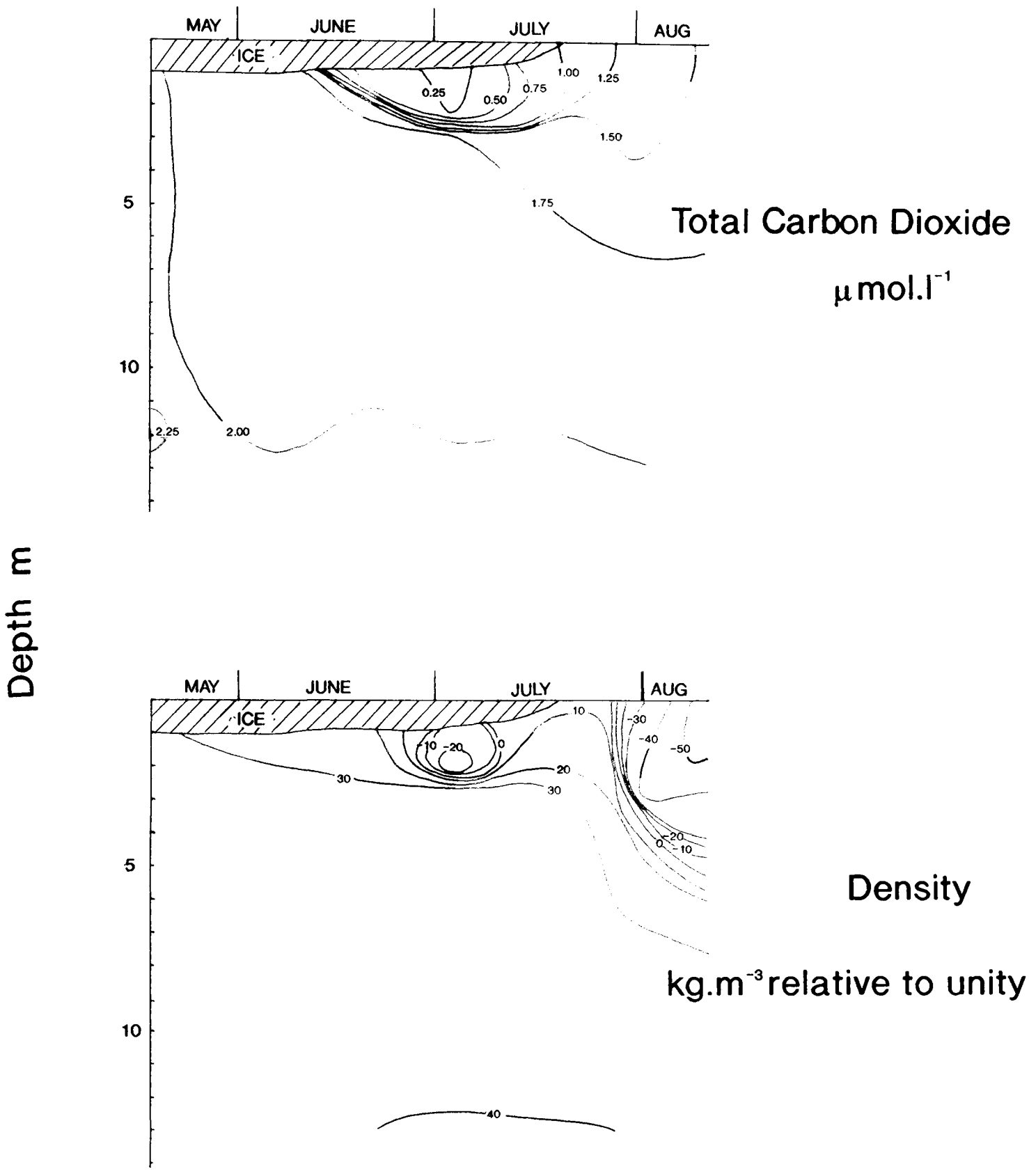
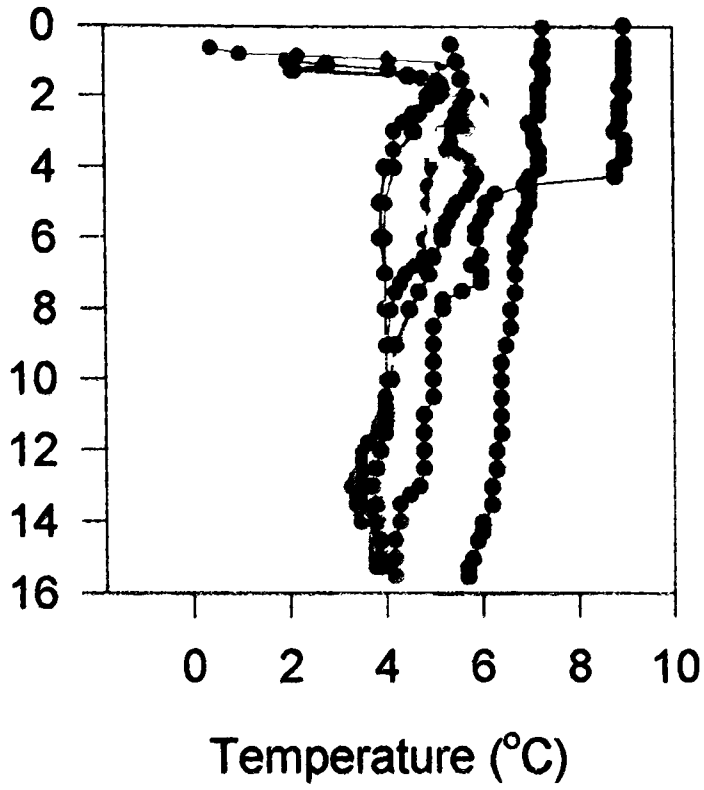
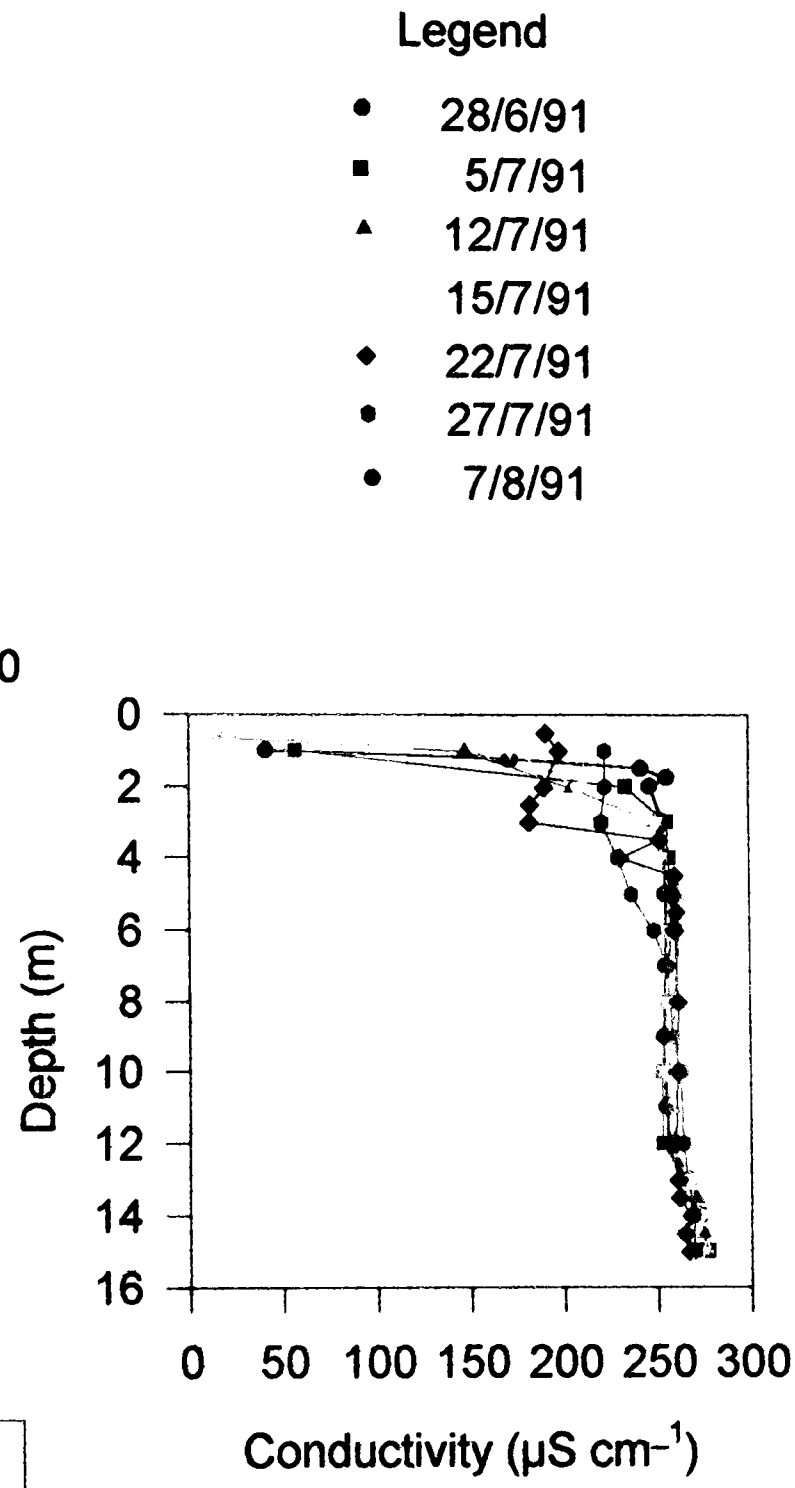


Figure 1.2 (continued) Isopleths of limnological data from Lake H in 1988





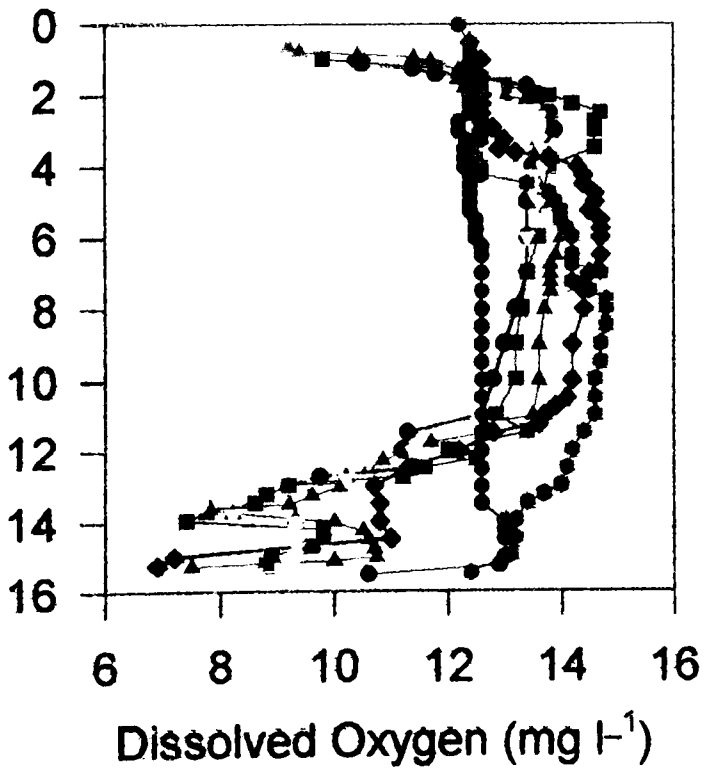


Figure 1.3 Limnological data from Lake H in 1991.

inflows were found to have a much higher average conductivity and temperature (ca. 200 $\mu S.cm^{-1}$, ca. 8 °C). As the thaw progressed, the surface layer became deeper and of higher conductivity. Over the period of open water and presumably due to solar radiation, the surface temperature climbed from 1.5 °C to 4.4 °C in a two week period and thereafter increased to 11 °C.

Combining the above into density profiles (Figure 1.2) reveals that two different forms of stratification were occurring. As the ice melted, a conductivity-driven stratification occurred in the top 2-3 m. In open water, a temperature-driven stratification became established in 1988 to roughly 5-6 m. Both stratification events would have restricted mixing of the lower water body. In the 1991 data (Figure 1.3) the thermally-driven stratification disappeared by 7 August after a period of bad weather and high winds. The contrast would indicate the importance of wind-driven mixing processes. The mechanism of change from a conductivity-driven stratification to fully mixed via a temperature-driven stratification could usefully be the subject of further research.

Snow covered the lake to a depth of 43-47 cm on 14 May 1988 and some remained until 16 June. In 1991 all snow had gone by arrival on 22 June. This snow probably insulated the lake in winter, such that the relatively thin ice thickness of ca.1 m resulted. It probably also prevented light from penetrating into the water column until mid June. Light penetration may explain the increase in dissolved oxygen at 3-5 m under the ice in early July. This is below the layer of virtually nutrient-free icemelt water but where

some light must still penetrate. Photosynthetic action may be occurring where there is an optimal combination between light and nutrient levels.

Evidence of biological action is also gleaned with respect to the sediments. There is not much evidence of increasing conductivity near the bottom at the end of winter, which indicates a low amount of bacterial activity in the glacial silt. This is also supported by the limited reduction in dissolved oxygen near the bottom, which in no way approaches anoxia, and this is coupled with a limited rise in total carbon dioxide.

A steady increase in the oxygen content near the bottom as the snow disappears and the ice melts may reflect the development of benthic algae and associated photosynthesis, although an inflow effect may also be responsible (Section 1.4.2). The subsequent decrease in late July may indicate grazing on this plant population by benthic fauna (predominantly chironomid larvae). Despite the overall increase in dissolved oxygen in the bottom ca. 2 m, there is always a reduction in the more immediate vicinity of the bottom indicating continuous sediment demand.

1.4.2 Under-ice water circulation - Lake H

As previously detailed, water of low conductivity appeared beneath the ice during the period of thaw. The low conductivity showed that its origin was melting lake ice rather than inflow water. The finer resolution achieved in 1991 data (Figure 1.3) tentatively

indicates that this water may be circulating on top of the lower, more conductive, layer with mixing occurring at the interface. Clues are given by the form of the temperature curves (Figure 1.3) where, under-ice, there is a slight drop in temperature at the same depth as the interface between the regions of high and low conductivity. This drop is as much as 0.7 °C on 12th July 1991, and the pattern is replicated on 12th July, 15th July and 22nd July but with ever-increasing layer depth. It is hypothesised that this is consistent with 0 °C meltwater from immediately beneath the ice moving laterally to the edge of the lake, mixing and returning over the top of the high conductivity layer.

With the disappearance of ice cover, solar radiation warms the upper 4 to 5 m of the water column during periods of low winds. A sharp thermocline is evident at 4-5 m but this disappeared within a few days of iceout in 1991, possibly due to the higher winds experienced that year. There is some evidence (Temperature curve, Figure 1.3, 27 July) that the mechanism for the heating of this upper layer is similar to that seen prior to iceout, since small temperature peaks are observed at the surface and thermocline depth. This is consistent with solar radiation heating the top few centimetres of the water column and then being wind-driven to the lake edge prior to mixing and returning over the colder, deeper layer. The tentative hypothesis is proposed that wind-driven circulation is primarily responsible for the changes from conductivity-driven stratification to fully mixed, via a temperature-driven stratification if the winds are gentle enough.

The temperature data (Figure 1.3, 12th July, 15th July, 22nd July) in the deepest part of the lake also shows a layer of relatively warm 4 °C water in approximately the bottom

metre of the water column during the thaw. The rise in temperature is as much as 0.5 °C meaning that heating via the sediments is unlikely. Simultaneously, there is a peak in dissolved oxygen at the same depth. This peak cannot be explained by the changes in temperature and conductivity alone and the basin is flat, indicating that morphometry is not responsible. This implies another potential water circulation as the likely mechanism where inflow, perhaps mixed with the circulating upper layer, is redirected under the "resident" water mass and accumulates in the deepest part.

Both of the above hypotheses for the circulation of water under ice cannot be proved or disproved using the current data. It is also apparent that the situation is complex with potential contributions from a large number of conflicting processes. Solar radiation, sediment heating, the effect of inflow water and wind are just some of the mechanisms which may have some effect on the under-ice environment (Welch & Bergmann 1985, Bergmann & Welch 1985, Hawes 1983). These physical and chemical features give clues as to the likely distribution of charr in the lake, which could then be tested by fish netting or echo-location.

1.4.3 Lakes A, B and C

Lakes A, B and C were subject to survey in less detail than Lake H due to their increased distance from base camp and the unavailability of a boat to take samples in open water. Nevertheless some limited sampling was achieved from the ice platform in 1991, and using direct readings from a DO_2/T probe operated by a swimmer. These lakes differ

from Lake H in that they have a more complex bottom composition as shown in Table 1.2. They were also isolated from the sea significantly before Lake H (Enclosure 1) and are shallower.

Temperature profiles in open water reflected water depth but varied between 1988 and 1991. In 1988 readings in open water showed that shallow Lake C reached a temperature of 12-13 °C throughout the water column, whereas Lakes A and B exhibited a solar-driven thermal stratification at around 4 m (similar to Lake H). In 1991, Lake C was not sampled but Lakes A and B became virtually isothermal at around 8 °C. This is as observed for Lake H, where it is supposed that the stronger winds prevalent in 1991 caused mixing of the entire water column. The relatively higher temperatures of these smaller lakes may mean that they are more productive overall than the deeper Lake H which, for similar reasons, may be most productive in its shallower regions.

From 1991 data, an increase in dissolved oxygen immediately beneath the ice in Lakes A and B during late June indicated some degree of photosynthetic activity, and this was correlated with a large number of *Cyclops* sp. found in the same location. Lake C was not sampled. From 1988 data, Lakes B and C achieved increasing oxygen levels with depth in open water, perhaps showing that photosynthetic activity from the benthic vegetation was the dominant biological process at that time. This was not apparent in Lake A which lacks benthic vegetation.

1.5 Landlocked Arctic charr - A Brief History

The Arctic charr, *Salvelinus alpinus* L., is circumpolar in its distribution, occurring in both anadromous and completely freshwater forms. It occupies fresh waters more or less continuously from the northernmost extremities of land to lakes at the latitude of the English Lake District (54° 30' N). Further south its distribution is discontinuous, occurring in the European Alps, the headwaters of Lake Baikal in Siberia, and in lakes along the eastern and western seaboards of North America. At the northern end of its range, from 71 °N to the limit of land at the northern end of Ellesmere Island (82 °N), non-anadromous Arctic charr is the only fish species encountered in fresh water. The anadromous form exists from the shores of the Arctic Ocean southward to approximately 60 °N latitude (Johnson 1980). South of this latitude it remains in fresh water even though it may have access to the sea.

The glacially sculptured nature of the entire area is primarily responsible for the physical circumstances of Borup Arctic charr and a study of the geomorphology of Midnight Sun Valley at the head of Oobloyah Bay allows rough dates to be suggested for their ecological history (Barsch 1981, Barsch *et al.* 1981). Arctic charr, presumably of anadromous stock initially, entered the lakes as they became differentiated from the sea; the formation of the lakes probably being associated with the glacial advance tentatively put at 20 000 years B.P.. Later, isostatic movement lifted Midnight Sun Valley to its present altitude some 80 m above sea-level. This created a physical barrier between the charr and the sea, and the charr consequently became landlocked. In this way,

landlocking occurred no longer ago than 15 000 to 20 000 yrs. and in any case no more recently than 6000 yrs. (Barsch pers. comm., Enclosure 1). The valley at the head of Essayoo Bay probably has a similar history although the short distance to the sea (300 m) and the low elevation (30 m) of the occupying lake means that landlocking might have occurred more recently.

1.6 Arctic charr - Major Scientific Questions

An important characteristic of the fish samples obtained from these undisturbed autonomous Arctic lakes, is that the length- and weight-frequency distributions are uni- or bimodal; and Griffiths (1994), who documented bimodality in 19 species of freshwater fish, reported a systematic increase in the frequency of bimodality with latitude. This modal character has given rise to considerable discussion as to the factors governing population structure in northern fish populations (Johnson 1976, 1983, Power 1978, MacCallum & Regier 1984, Sparholt 1985, Riget *et al.* 1986, Vanriel 1989). Both males and females can exhibit bimodality, unimodal populations remain common at all latitudes, and modal size may vary. Individuals associated with the smaller mode may or may not be reproductively competent, and sexual dimorphism is observed in both size and reproductive strategies. The awkward, but standard, terminology for fish associated with each of the size modes is generally used (e.g. Klemetsen & Grotnes 1980). The members of the smaller mode are termed "Dwarfs", whilst the larger fish are "Normals".

There is also a complex of questions on the genetic relationships between the alternate modes (the "charr problem" - Nordeng 1983) in that morphological differences, for example in gill raker counts, are observed. In the majority of studies designed to test for genetic divergence (e.g. Hindar *et al.* 1986, Danzmann *et al.* 1991, Hartley *et al.* 1992, Snorrason *et al.* 1989) a variety of molecular techniques have, however, failed to provide conclusive evidence for divergence in sympatric stocks. A question of considerable theoretical importance is whether these different morphs arose sympatrically, which would cast doubt on the accepted view that incipient speciation occurs only in isolation; or whether they evolved in isolation, eventually coming together in one location through migration.

1.7 Thesis Structure and Collaborations

Whilst individual contributions from other people are detailed in the Acknowledgements, the contribution of both fieldwork and theory to this thesis means that some explanation is needed as to its structure. Chapter 2 details the fieldwork on the population structure, ecological segregation and reproductive strategies of charr. Chapter 3 examines the parasite communities and their intermediate hosts and discusses their relevance to the fish ecology. Chapter 4 is a link between the fieldwork and theory. It describes the indirect evidence for a third modal size of charr in one lake, and then poses four questions for theoretical analysis. The subsequent chapters are both theoretical and deal with growth patterns, population structure and their genetic consequences. The overall conclusions are discussed in Chapter 7. A glossary of specialist terms is included.

2. Population Structure, Ecological Segregation and Reproduction

Arctic charr Fieldwork

Supervised by Dr. Lionel Johnson

2.1 Chapter Abstract

The landlocked populations of Arctic charr in four lakes on Northern Ellesmere Island (80 °N) were found to consist of two distinct sizes: "Dwarf" and "Normal" charr. Both groups attained sexual maturity but differed in appearance and habitat. The smaller Dwarfs, occupying the more marginal habitats, retained their parr-markings; the larger Normals had the general characteristics of smolts, being more silvery and without parr-marks. In their juvenile stages, the charr destined to become Normals were externally indistinguishable from reproductive Dwarfs. Although fish in the larger group were capable of cannibalism, this was rarely observed. In general, the Normals were older than the Dwarfs but great variation in size at a given age resulted in certain age classes containing representatives of both groups. The population structure varied considerably between lakes; a high proportion of Normal charr correlated well with a high growth rate in the first few years of development. Generally, the different modal sizes were found in different parts of the lakes and spawning was infrequent relative to more southerly systems.

2.2 Introduction

This chapter introduces the basic survey fieldwork conducted between May and August 1988. It has largely been published in a joint paper, "Population structure, ecological segregation and reproduction in non-anadromous Arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in the Canadian high Arctic" Journal of Fish Biology (1991), **38**, 123-147. Much of the introduction, study area and discussion sections of the paper have been extracted and presented in other chapters. A copy of the paper is enclosed with the thesis.

2.3 Materials and Methods

Lake H was under observation from mid-May to late-August 1988. The study was primarily designed to examine possible changes in the structure or distribution of the Arctic charr population over the course of the summer season. The size of this lake enabled different habitats to be identified and fished separately, thus permitting investigation of habitat segregation and differences in food consumption. Lakes A, B and C were sampled during August to examine the possible existence of differences attributable to a geographic gradient such as altitude.

2.3.1 Fishing methods

Fishing in Lake H was carried out during three discrete periods: late-May, mid-July and mid-August. During the latter half of May, vertical set lines with baited hooks at known depths were fished through holes in the ice. In an attempt to overcome any possible bias with respect to hook size both small and large hooks were included in the rigs. Funnel traps were also set at different depths.

During the mid-July and mid-August sessions, monofilament multimesh survey gillnets were used in pairs, one floating and the other set on the bottom, one above the other. The nets were set roughly parallel to the shore and fished for a period of 24 h.. The depth of setting was determined by echo-sounder.

In Midnight Sun Valley, Lakes A, B, and C, were visited in the first half of August and sampled in similar fashion by setting a survey bottom net perpendicular to the shore by swimming.

The gillnets were 32 m long, constructed of eight 4 m, monofilament panels, each 1.5 m deep and each being of a different mesh size. The mesh sizes were (stretched measure) 18, 24, 32, 43, 48, 71 and 90 mm arranged in random order in each net.

2.3.2 Treatment of samples

The fork length of all fish was measured to the nearest millimetre. The fish were, if large, weighed to the nearest 5 g or, if less than 100 g, weighed to the nearest 1 g. Reproductive status, stomach contents, physical condition and parasite infestation were assessed. Sex was recorded and the degree of sexual maturity assessed according to the method of Kesteven (1960). Food items were analysed in the field and assessed quantitatively using the points method of Hynes (1950), a full stomach being allocated 10 points on a scale of 1 to 10. The Fulton condition factor (K), a measure of the 'fatness' of fish (Hile 1936, Le Cren 1951) was determined from the formula:

$$K = \frac{W x 10^3}{L^3}$$

where W = weight (g), and L = length (mm).

Sagittal otoliths were removed and stored dry for later age determination in the laboratory. Otoliths were read according to Nordeng's (1961) interpretation.

Parasites were collected from each fish. This operation formed a major portion of the effort expended on each fish, partly because relatively little work has been done on parasites at this latitude, and partly to provide information on ecological relationships. The parasite work is presented in Chapter 3.

2.4 Results

2.4.1 Morphology and definition of types

The majority of the length- and weight-frequency distributions of the samples was bimodal in form (Figures 2.1, 2.2, 2.3, 2.4), with the size modes corresponding to fish of different appearance. Charr in the smaller mode, in all lakes, had the appearance of parr, characterised by approximately ten bluish vertical bars along the flanks. The overall coloration was a well-camouflaged green with a white belly. Photographs are at Figure 4.2. To remain consistent with the rest of the literature (e.g. Klemetsen & Grotnes, 1980), fish of this type will be referred to as "Dwarfs".

In all but one of the lakes, a second mode of larger fish was also present. These larger fish had the appearance of smolts with a grey-green back and bright silverpink flanks. Eyes were relatively larger than in the Dwarf and larger specimens had hooked lower jaws with an impressive array of backward-sloping teeth. Toward spawning time, the males attained an orange coloration with white-edged, bright red fins. These are known as "Normal" charr. Fish in the pre-spawning state with maturing gonads were observed in both Dwarf and Normal categories. A number of fish, rarely caught, were of intermediate size and coloration.

2.4.2 Habitat segregation and food (Lake H)

Each type was loosely found to occupy a different habitat, as indicated by location of capture and stomach contents. The nature of this segregation varied as the opportunities for feeding changed over the period of the study. The overall segregation indicated that the Normal charr command the best feeding areas, while Dwarfs make best use of what was left.

The benthic fauna, which forms the main diet of the charr is dominated by chironomid larvae. The most abundant species were *Paracladius alpicola* (Zetterstedt), *Heterotrissocladius* n.sp. and *Paratanytarsus natvigi* (Goetghebuer). Also present were *Heterotrissocladius subpilosus* (Kieffer), *Microspectra* sp. and a new species of *Stichtochironomus*. The trichopteran, *Apatania zonella* (Zetterstedt) and aquatic mites (Acari) were also present.[2]

During late-May, while the lake was still ice-covered, Normal charr were found in the colder upper layers of the lake and most had empty stomachs. Two out of 25 were found to contain Dwarfs. By their size, it seems that most Normal charr are capable of consuming Dwarfs when opportunity arises, although relatively few instances were recorded. Dwarfs were found to be bottom dwelling, feeding mainly on chironomid larvae. (Figure 2.1 & Table 2.1).

[2] See Enclosures 3 and 4

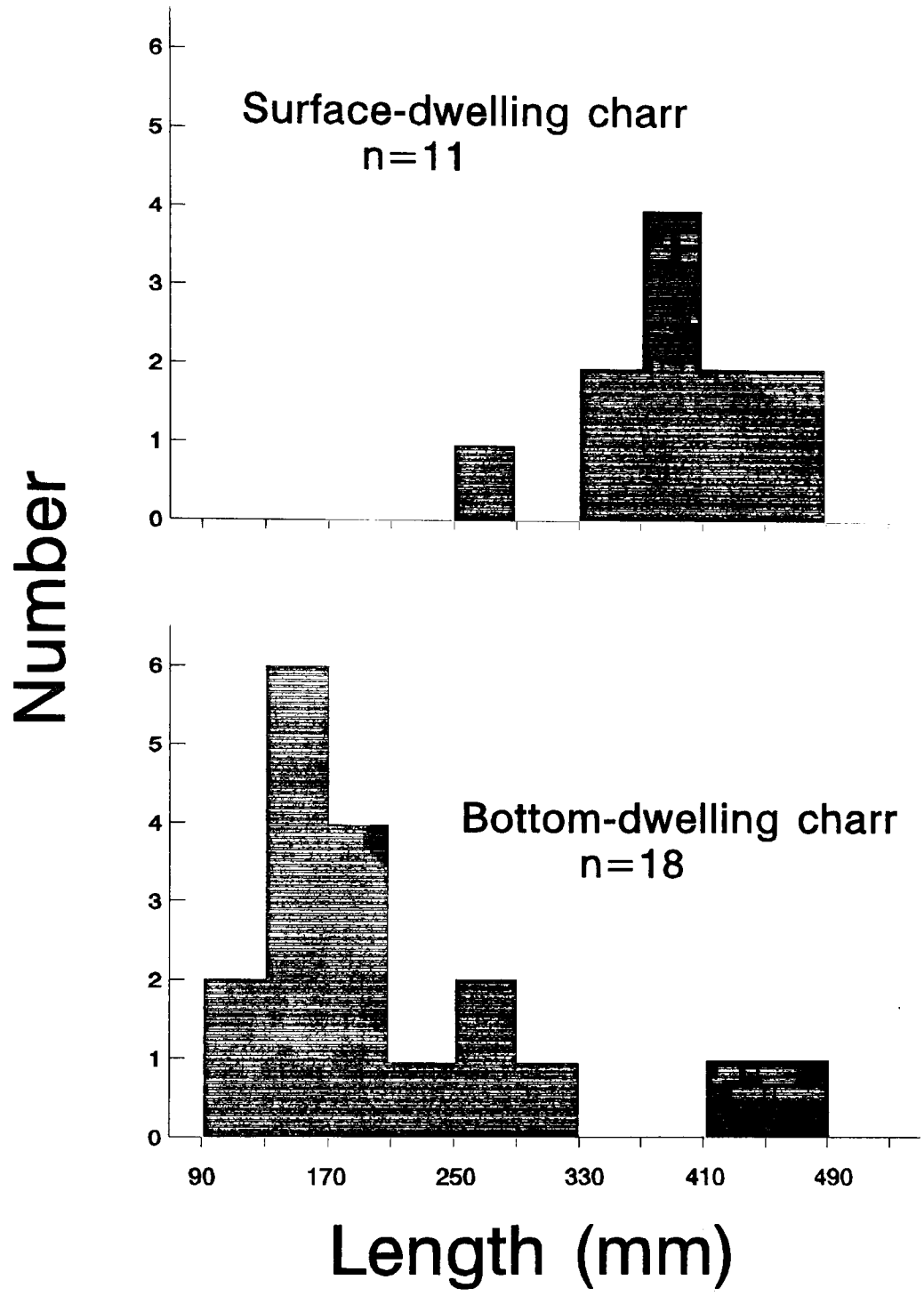


Figure 2.1 Length-frequency diagrams showing depth distribution of Arctic charr caught below the ice in Lake H, during the latter part of May 1988. Segregation into two distinct modal sizes at this time of year is by water depth, the smaller charr adopting a bottom-dwelling existence, with the Normals occupying the coldest water immediately beneath the ice.

	Chironomid larvae	Trichopterid larvae	Water mites	Zooplankton	Fish	Empty
Dwarfs (n = 18)	64	11	5	0	0	20
Normals (n = 11)	6	6	10.5	2.5	7.5	67.5

Table 2.1 Niche segregation of morphs by stomach contents in late-May. The figures indicate the percentage of fish containing the given food item. A large proportion of the Normal charr had empty stomachs, whilst the Dwarfs were mainly feeding on Chironomid larvae.

When the ice finally cleared from the lake on 21 July, Normal charr were found in those areas of the lake where the gentle, prevailing south wind allowed them to feed selectively on enormous numbers of large chironomid pupae trapped in the surface film or in the remaining ice. As a consequence, Normal charr dominated the shoreline zone and were frequently observed surface feeding. The Dwarfs were restricted either to the shallowest water less than 1 m deep, or the outlet zone where feeding was not as good as along the shoreline. Stomach contents of the Dwarfs indicated more catholic feeding habits; they exhibited a wider variety of organisms than Normal charr but a lesser degree of fullness. The deepwater zone was almost barren of fish and attempts to catch pelagic fish by suspending a bottom net in midwater proved fruitless. Figure 2.2 indicates the habitat segregation by zone, and Table 2.2 by volume of stomach contents.

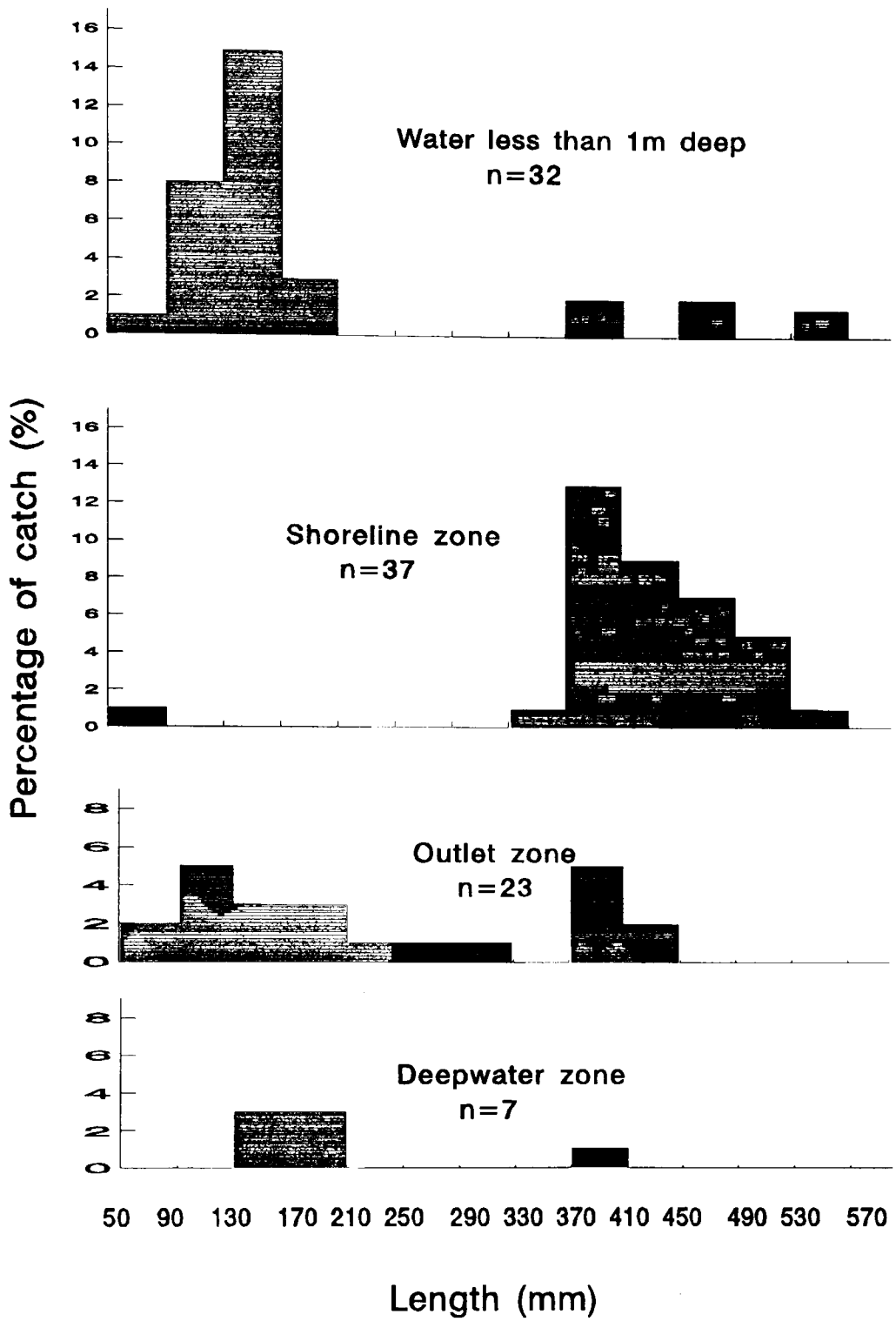


Figure 2.2 Niche segregation by length of Arctic charr in Lake H during the open water period in mid-July 1988. The Normals dominate the shoreline zone, with the Dwarfs restricted to shallow water or the relatively infertile outlet zone.

	Large chironomid larvae	Medium chironomid larvae	Small chironomid larvae	Algae	Other	Empty
Dwarfs (n = 46)	4	18	50	0	5	23
Normals (n = 54)	90	1.5	3	1.5	0	3

Table 2.2 Niche segregation of morphs indicated by stomach contents in mid-July. The figures represent the percentage overall volume of given item within stomachs.

In the final session, during mid-August, with winter fast approaching, spawning was still some time away. Habitat segregation was indicated by the almost complete disappearance of the Dwarfs (Figure 2.3). Plankton net hauls 1 to 2 weeks previously had qualitatively indicated a large increase in the availability of zooplankton so it is possible that the Dwarfs were feeding scattered throughout the pelagic region. The Normal charr were now spread out more evenly around the edge of the lake and were no longer surface feeding. The deepwater zone was still almost devoid of fish.

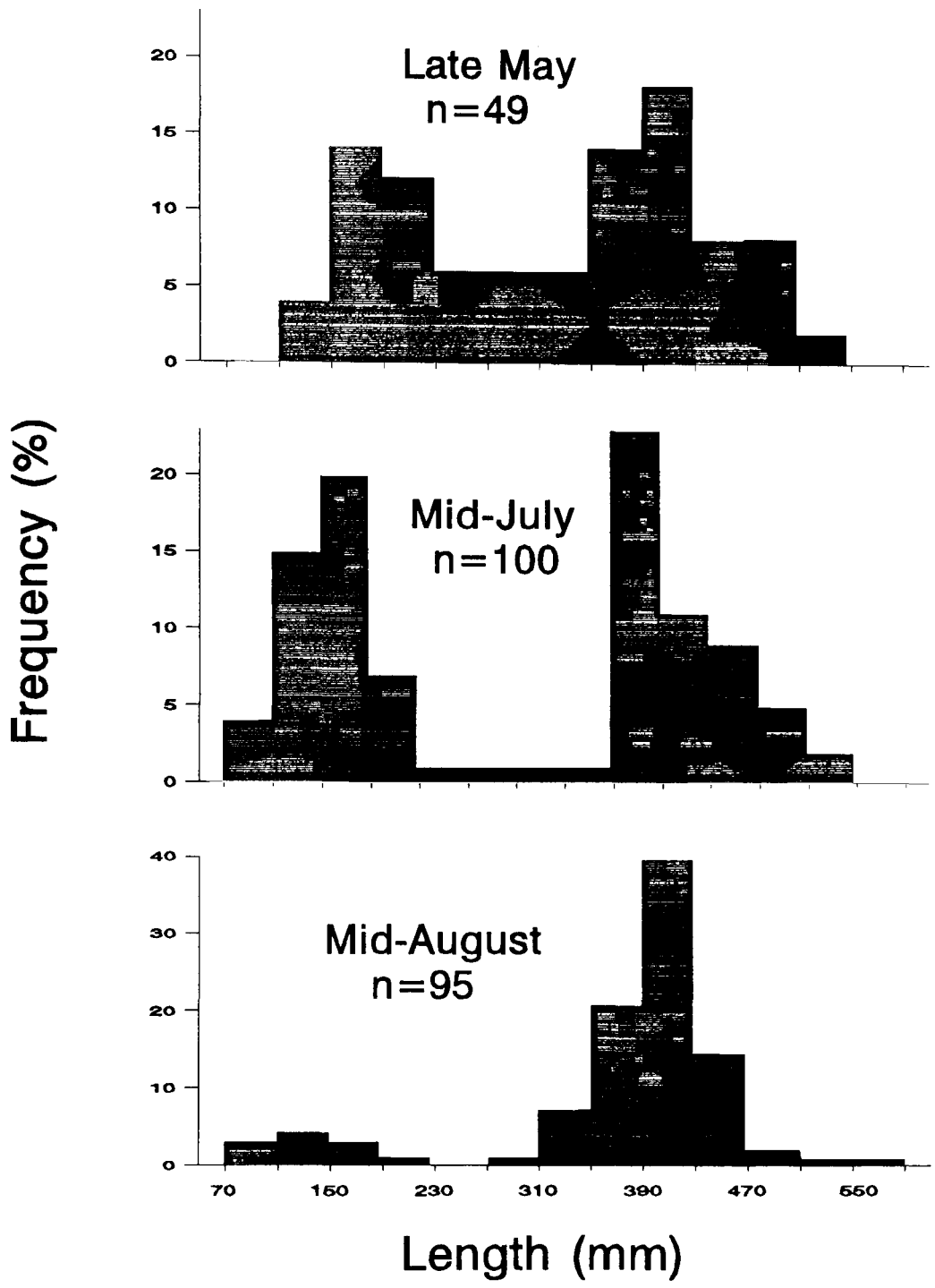


Figure 2.3 Length-frequency distribution of Arctic charr in Lake H during May, July and August, 1988. The data for May were collected by hook and line, and for July and August by multi-meshed gillnet (see section on Methods for details). Few Dwarfs were captured in the final sampling session despite using similar fishing methods to previously.

2.4.3 Length-frequency distributions

Length-frequency distributions for all lakes are shown in Figure 2.4. Apart from Lake A (the one at highest elevation) which contained only Dwarfs, the diagrams all show bimodal (or tentatively trimodal) distributions. The actual values of the modes vary from lake to lake, as does the relative abundance of Dwarf and Normal charr.

The males in the Dwarf populations are smaller than the females. This is especially noticeable in Lake A where the modal length of females is 110 mm compared with 100 mm for males. In Normal charr this relationship is reversed with males, on average, being larger than females (Figure 2.5). This inversion has previously been noted by Jonsson & Hindar (1982).

2.4.4 Age-frequency distributions

For those lakes with a bimodal length-frequency distribution, the age distribution was also bi- or trimodal (Figure 2.6). The immediate conclusion might be either that some fault in the method of ageing the fish from otoliths was responsible, or that there was bias in the sampling procedure, with fish in the middle age group apparently missing.

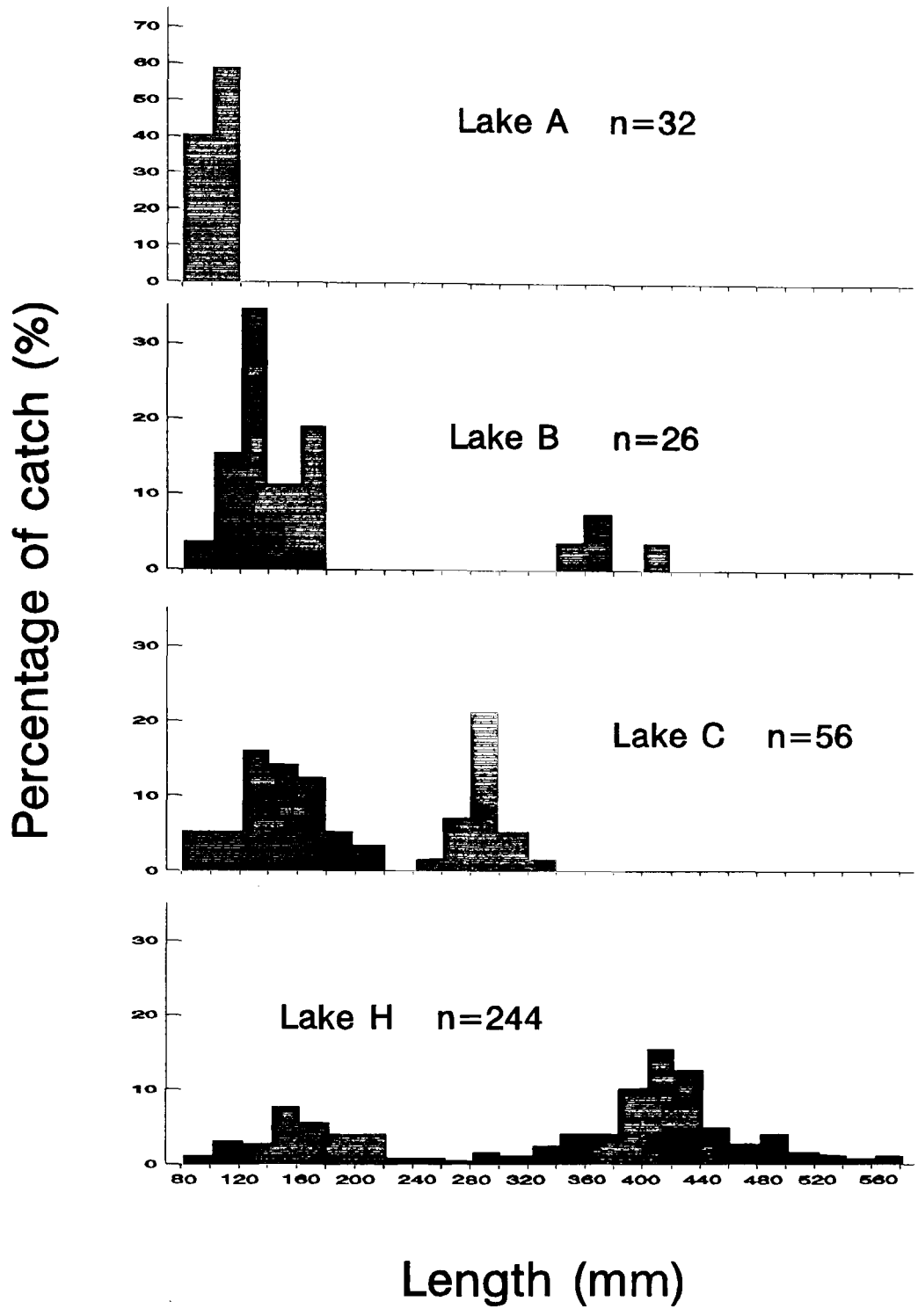


Figure 2.4 Length-frequency distribution of Arctic charr for Lakes A, B, C and H. The data for Lake H represent the combined results for all fishing periods. The length and relative numbers of the size modes vary between lakes.

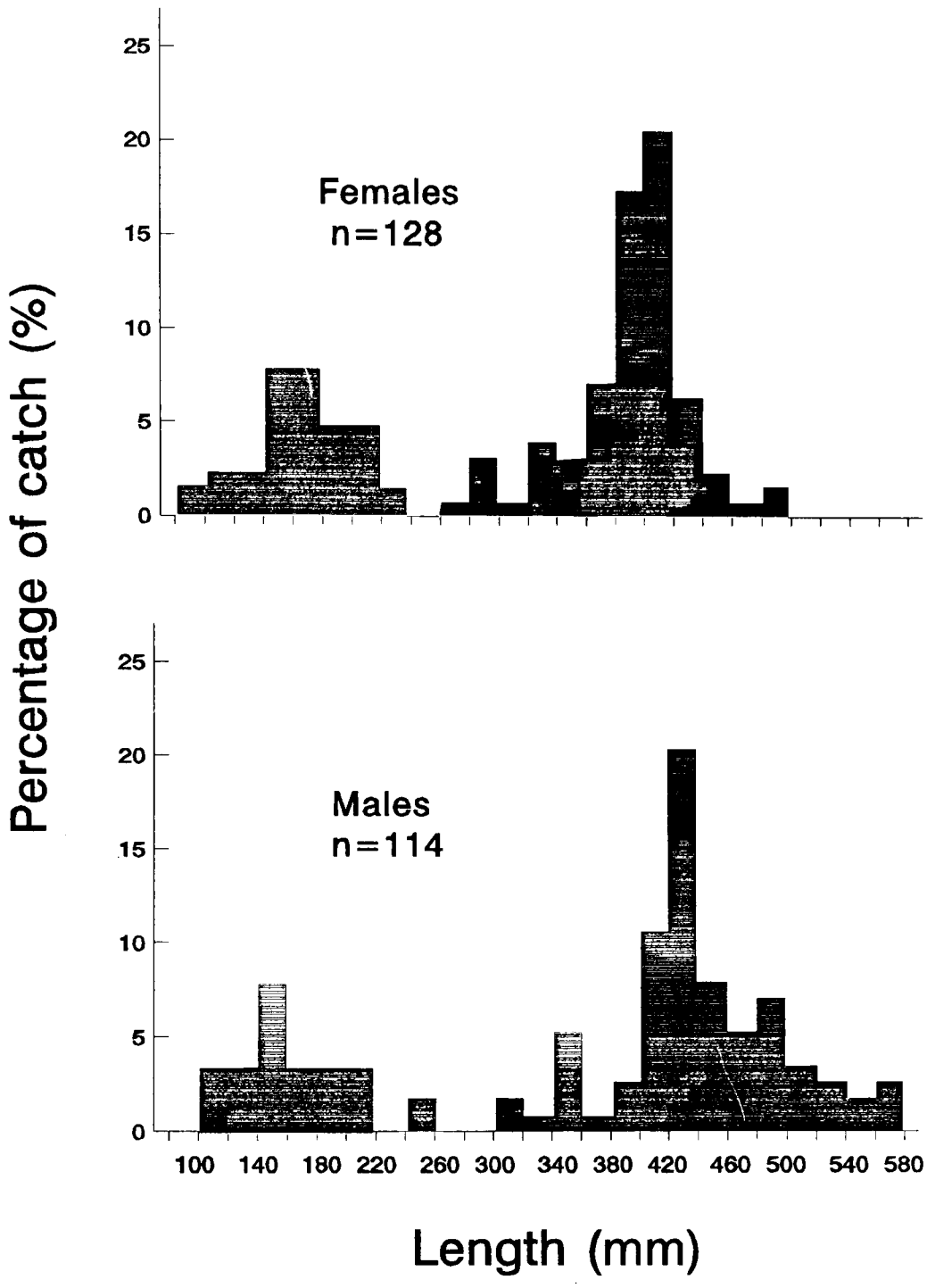


Figure 2.5 Length-frequency distributions, as a percentage of catch, for male and female charr from Lake H. Based on combined data for all fishing periods. Normal females are smaller than Normal males, but this is reversed for Dwarfs.

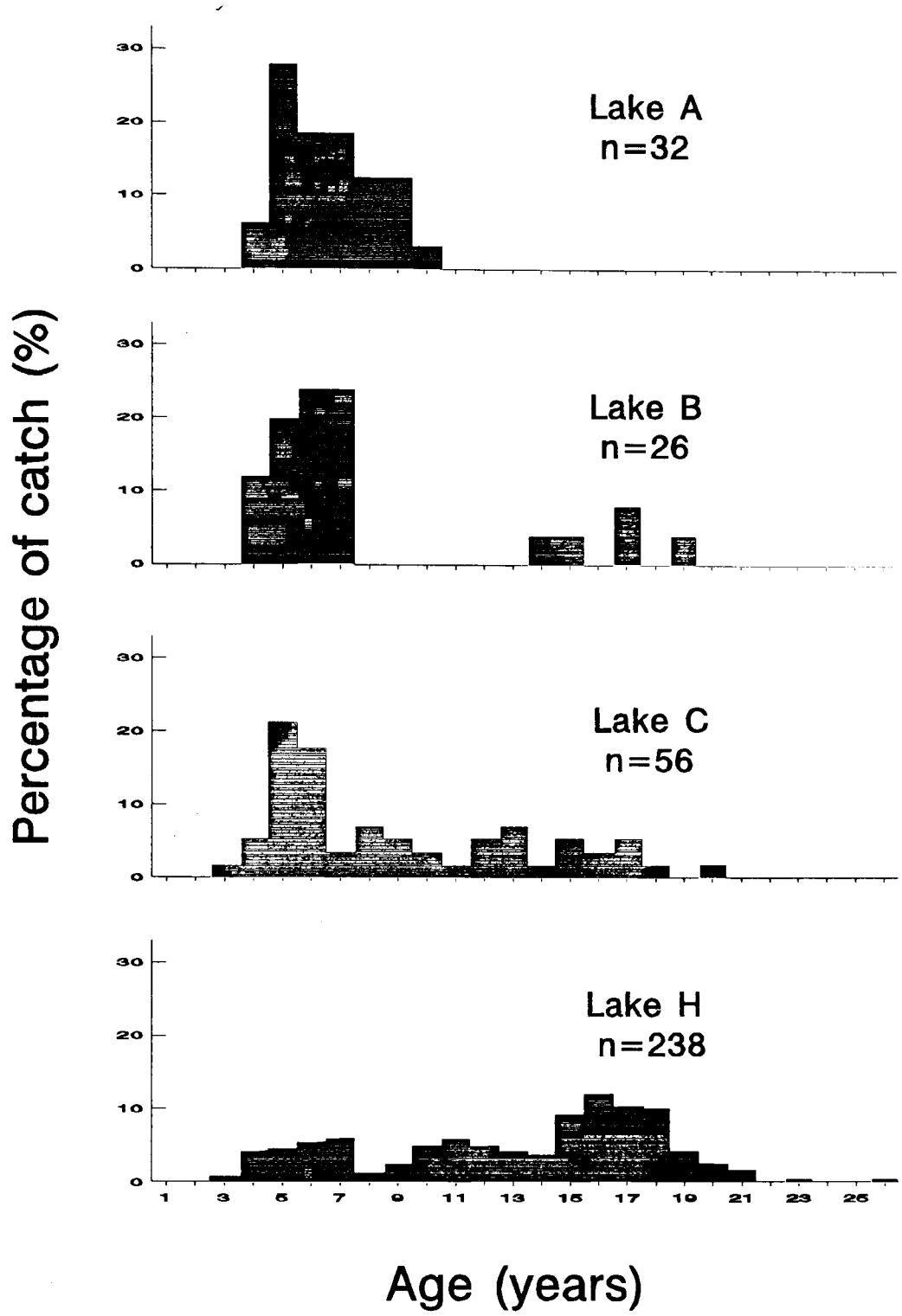


Figure 2.6 Age-frequency distribution of Arctic charr from Lakes A, B, C and H.

2.4.5 Growth

Considerable variation in size is apparent at any given age. Length and age are the usual axes for presenting such information, but weight and age is used at Figure 2.7. This is because weight is more closely associated with energy stored as somatic tissue than length and the significance of this is discussed later. The good correlation between length and weight (Section 2.4.6) indicates that little additional information would be gained by presenting both sets of data and this is confirmed by plotting.

2.4.6 Length-weight relationship and condition

For Lake H, the length-weight relationship was determined by linear regression to be

late-May: $\log_{10} W = -5.17 + 3.01 \log_{10} L$ (r = 0 99; n = 49)

mid-August: $\log_{10} W = -4.94 + 2.95 \log_{10} L$ (r = 0 99; n = 95)

An increase in weight is apparent between May and August for both size modes. 95% confidence intervals indicate that the lower modal length value (180 mm) increased from between 39.2 g and 46.5 g, to between 48.4 g and 54.9 g; and the upper modal value (420 mm) from between 512.4 g and 586.1 g, to between 608.2 g and 650.2 g.

Length versus condition is shown for all lakes in Figure 2.8. In general, condition declines with length. Where Normal charr are abundant they have a relatively high condition factor. In Lake H, condition drops for intermediates between the two modal size classes.

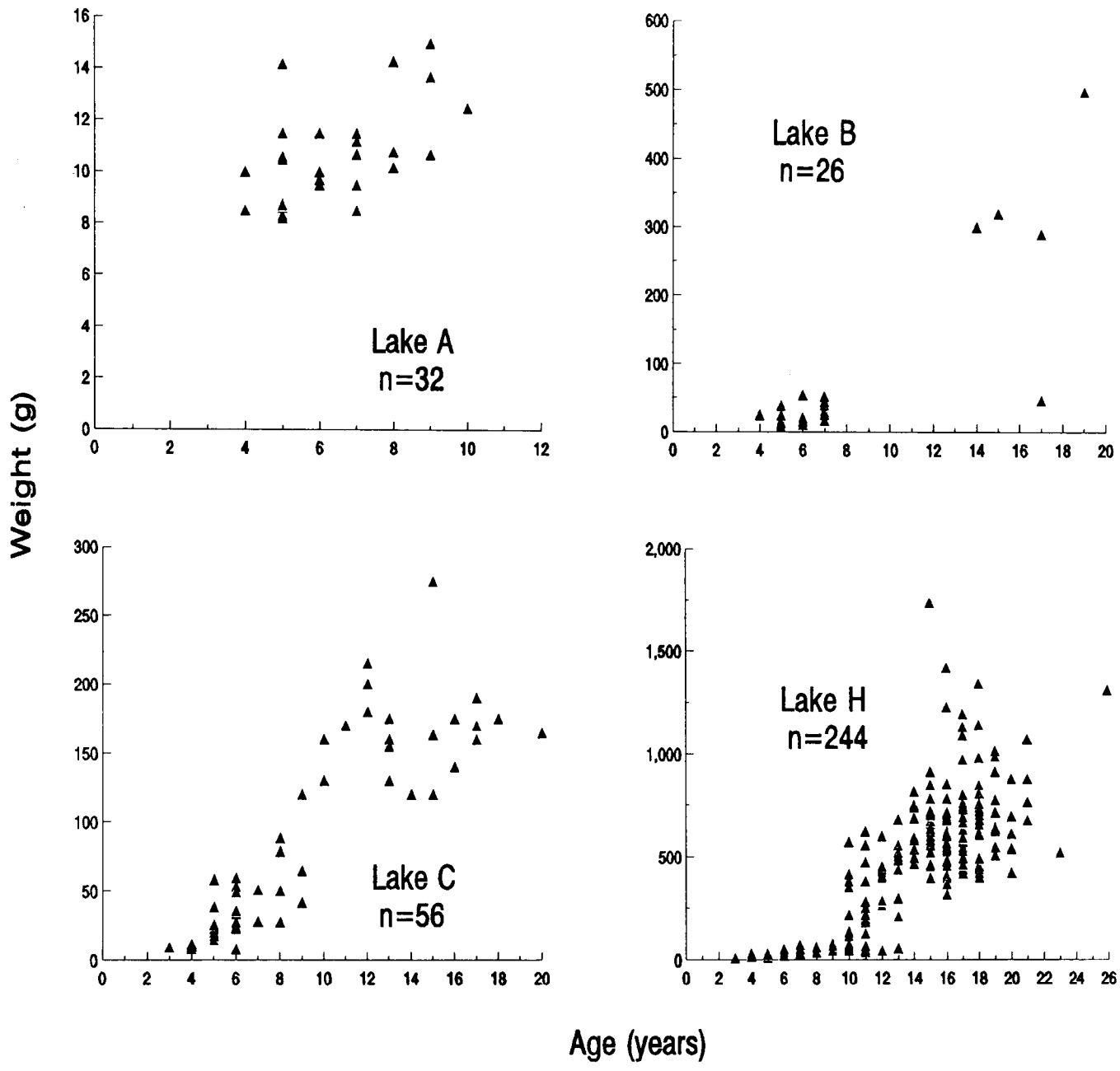


Figure 2.7 Weight against age for Arctic charr from Lakes A, B, C and H. Note that different axes are used in each plot.

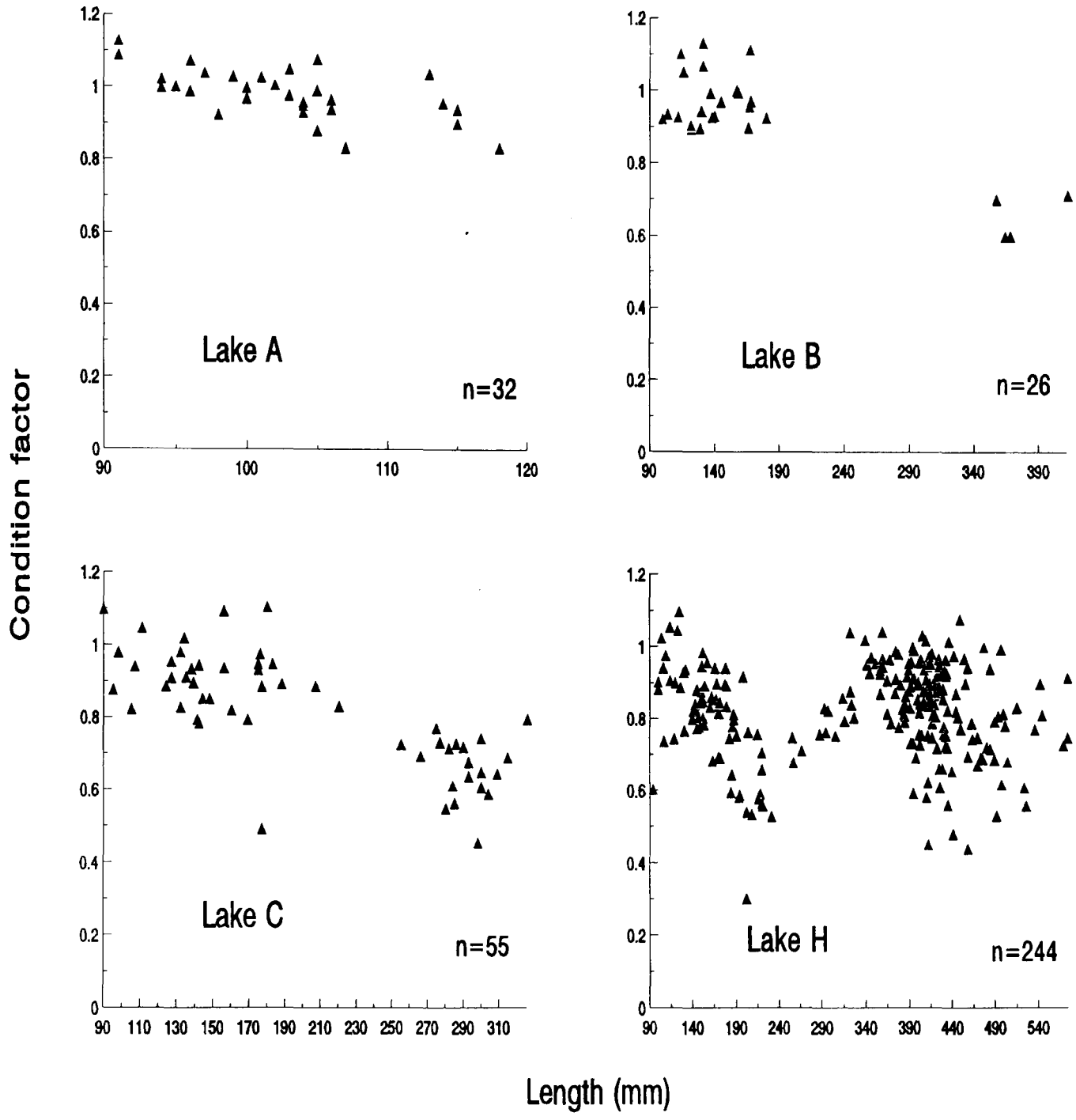


Figure 2.8 Condition factor (K) against length for Lakes A, B, C and H. In general there is a trend towards decreasing condition with increasing length.

2.4.7 Sex ratios

The sex ratio for the charr in all lakes is given in Table 2.3. The probability (P) has been calculated assuming a binomial distribution and the null hypothesis that the sexes are equally represented. There appears to be a trend in which there is a decreasing probability of the sex ratio being equal from Lake A, through B and C to H; however, the significance of this trend is not apparent.

	Lake A	Lake B	Lake C	Lake H
Dwarfs				
Males	15	11	11	31
Females	17	11	18	44
P	0.13	0.17	0.06	0.03
Normals				
Males	/	1	7	83
Females	/	3	15	85
P	/	0.25	0.04	0.06

Table 2.3 Sex ratios of Arctic charr in Lakes A, B, C and H. The probability (P) is calculated for the null hypothesis that the sex ratios are equal and assuming a binomial distribution.

2.4.8 Age at maturity and frequency of spawning

Table 2.4 shows the age of the youngest fish found to be mature in each of the lakes differentiating between males and females. It also shows the frequency of fish identified as maturing in 1988 relative to the total number of fish of the same sex and type older than the youngest mature fish. The reciprocal of this figure gives an indication of the frequency of spawning once the age of first maturity has been reached. Maturity is defined as potentially spawning in the year of study. Care must be exercised in interpreting these data; for example, a spawning frequency of once every 10 years, as determined for Normal females, indicates that spawning occurs, on average, only once in a lifetime.

Lake A is particularly important because all members of its population can be classified as Dwarfs. In the other lakes the data are less clear because of the impossibility of distinguishing between mature Dwarfs and immature Normal charr. In Lake A, almost all the males caught were mature, implying an annual spawning cycle, whereas only one quarter of the females were mature, indicating a 4-year cycle. Lake H provides the best picture of Normal charr. Once again, the proportion of maturing males is twice that of females. Both sexes are reproducing infrequently relative to more temperate systems, where an annual cycle is commonly observed.

	Observed age of first maturity (years)		Frequency of spawners older than age of first maturity		Sample size of fish older than observed age of first maturity	
	Dwarf	Normal	Dwarf	Normal	Dwarf	Normal
Males						
Lake A	4	/	0.75	/	15	/
Lake B	4	/	0.55	/	9	/
Lake C	9 (1 only)	/	Insuff. data	/	/	/
Lake H	5	15	0.21	0.22	23	54
Females						
Lake A	5	/	0.24	/	17	/
Lake B	/	/	/	/	/	/
Lake C	/	15	/	(0.33) Insuff. data	/	6
Lake H	7	13	0.15	0.09	19	55

Table 2.4 Summary of reproductive tactics by sex and type for Arctic charr in Lakes A, B, C and H.

2.4.9 Gonad weight and fecundity

Figure 2.9 shows the gonadosomatic index (GSI) plotted against length, for mature fish of both sexes. These scatter diagrams represent mature fish from all four lakes plotted on the same axes in order to provide a wide spread of data. From these data a number of regressions were calculated:-

Males: $\log_{10}GSI = -5.07 + 2.44 \log_{10} L$ (r = 0 982; n = 34)

Females: $\log_{10}GSI = -7.36 + 3.45 \log_{10} L$ (r = 0 967; n = 18)

$\log_{10}$ (no. of ova) $= -3.24 + 2.45 \log_{10} L$ (r = 0 985; n = 10)

With due care in interpretation due to the data being gathered some weeks before spawning, these equations imply:-

1. The contribution of ovarian tissue to each ovum in females increases linearly with fish length.

2. The number of ova increases with length. Because egg diameter increases with fish length (fish 100 mm in length had egg diameters of approximately 3 mm, whereas a 400 mm fish had egg diameters of 5 mm), it is concluded that both actual fecundity and weight per ovum increase with fish length.

3. In males, the absolute gonad weight increases in parallel with the number of ova in a female of equivalent length. This means that if a male spawned with a female of the same length it would release a similar number of sperm per ovum regardless of its own length.

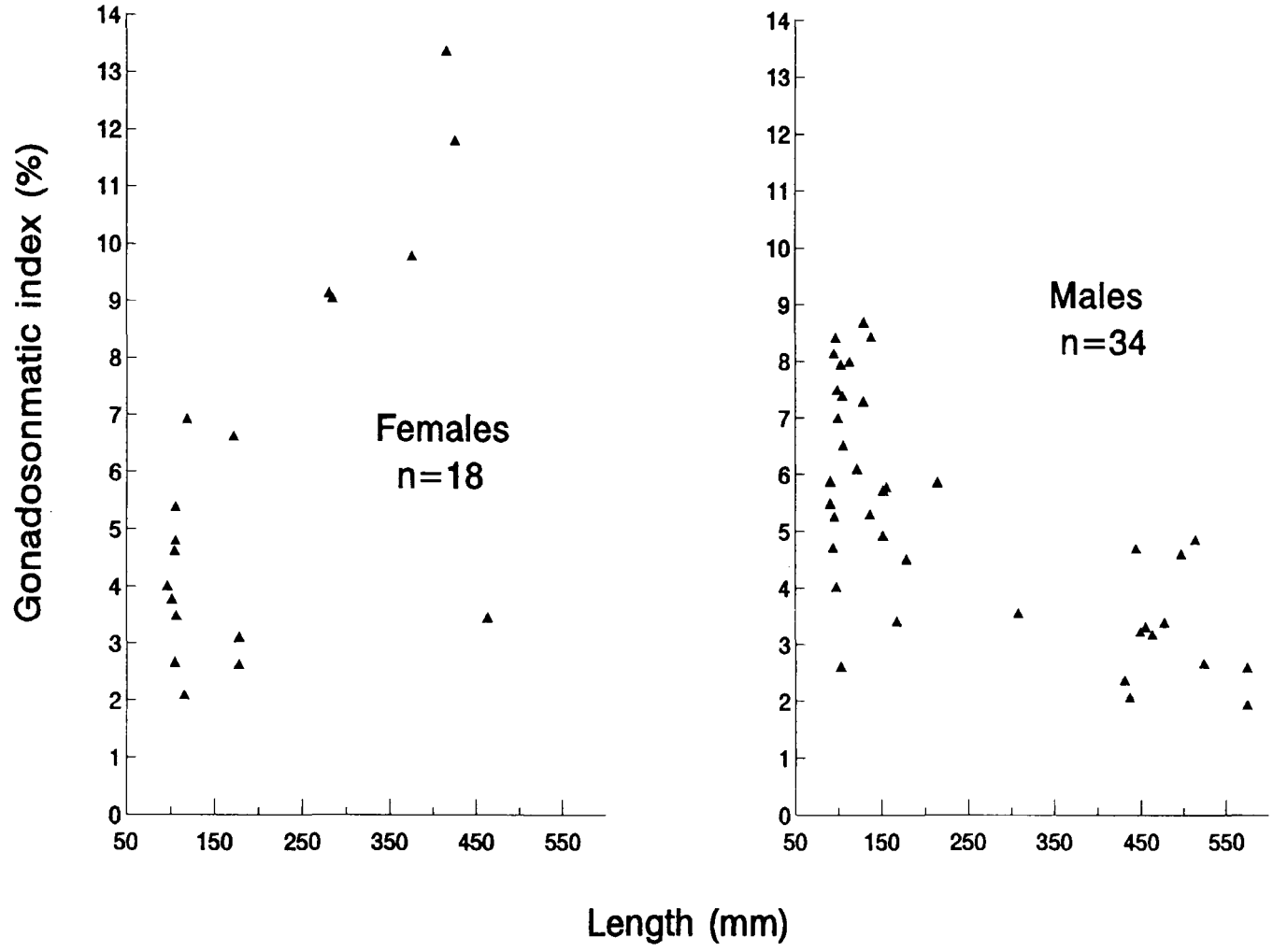


Figure 2.9 Comparison between sexes based on gonadosomatic index (gonad wt./ body wt.) against length, for mature fish from all lakes. The anomalous value for the largest female caught results from an incompletely developed ovary: the posterior region only had developed.

2.4.10 Gill rakers

In Lake H, Normal charr had a mean gill raker number of 25.8 (n = 177) which a *t*-test showed was significantly higher than the 22.3 (n = 120) found in Dwarf charr.

2.5 Discussion

2.5.1 Gillnet selectivity and other errors

The representativeness of a sample from a fish population obtained by gillnetting has been much discussed in the literature (e.g. Ricker 1975, Johnson 1976, 1983; Power 1978, Sparholt 1985). The pertinent question is the extent to which mesh selectivity biases the sample obtained. With adequate data it is possible to make theoretical estimates of the bias introduced by each mesh size. However, the manner in which the nets are used and the way in which the results are interpreted are, potentially, a much greater source of error.

Within a given lake it has been found, in practice, that the catch of different gillnet gangs made up of different mesh sizes yields similar results. Conversely, where identical gear is used for sampling in different lakes, the actual modal values exhibit considerable variation. The modal structure itself cannot, therefore, be attributed either to chance or to gillnet selectivity. Only in the case of the smallest fish (< 70 mm) were the low numbers probably the result of gillnet selectivity.

It is also evident that behaviour significantly influences the catch statistics. Big, fast-swimming predatory fish which patrol large areas are much more likely to be caught in a static net than slower, smaller fish. Pelagic fish are inclined to shoal with an unknown effect on catch statistics. In a previously undisturbed population in Keyhole Lake, Victoria Island, small Arctic charr were caught in greater abundance when the majority of the large members of the population had been removed (Vanriel 1989).

Thus, the samples produced by gillnets are representative only of the habitats in which they are fished effectively and the samples produced contain an unassessable bias towards large fish caused by behavioural differences. The actual magnitude of a sample in any given environment, it may be assumed, will also be proportional to the density of fish present. Ultimately, gillnets, for all their perceived disadvantages, are by far the most effective fishing gear available for use in Arctic conditions.

Another possible source of error which may effect interpretation of the data is determination of individual age. This was achieved via a 'crack and burn' technique using otoliths, and difficulty was experienced due to the slow growth of these long-lived populations. This slow growth means that the opaque rings representing the summer growth cycle are close together and hard to discriminate. Despite this difficulty, an error of even a few years in the older fish is likely to have little relative effect due to their great age.

2.5.2 The modal structure

The population structures of the Arctic charr in the four study lakes are distinguished by their uni- or bimodal (sometimes tentatively trimodal), length- and age distributions and the great age of individuals. In three of the four lakes examined two morphs exist sympatrically, with each morph containing reproductive individuals. In the fourth lake only the Dwarf form, is found. Considerable difference in modal weights between morphs was observed both within and between lakes.

The effects of sampling bias due to gillnets has previously been discussed and, indeed, there is some evidence for an undersampled intermediate-sized pelagic fish in Lake H (Section 4.3). It is, however, likely that this fish constitutes yet another size mode rather than filling a gap in what would otherwise be a unimodal distribution. Evidence from more heavily-studied systems show that these modal characteristics are typical of arctic or high mountain lakes (Johnson 1972, 1976, 1980, 1983, Pechlaner 1984, Sparholt 1985, Riget *et al.* 1986, Vanriel 1989).

The potential mechanisms for maintenance of bimodality are many (Huston & de Angelis 1987) but the theory of size-structured populations (Werner & Gilliam 1984) offers some common currency to all of them. In this theory it is supposed that an individual schedules its life history to maximise the ratio of energy acquisition rate to mortality risk. Size is one of the most important parameters in determining this ratio and there are only a limited number of ways in which it can be optimised within a natural system.

Thus, for example, some types of prey items may not be energetically or physically viable until a fish reaches a certain size. Alternatively, a fish may become more or less vulnerable to predators as its size changes. Even without being able to quantify the different optimal sizes associated with each available food item, different fish size modes would be expected to be associated with different food types. This is observed in the Borup lakes and Forseth *et al.* (1994) documents the energetic basis of one such size-related diet shift.

Uni- or bimodal structures are not confined to northern species. Johnson (1994) has shown that a wide range of species populations in undisturbed, relatively autonomous ecosystems, in various parts of the world, show similar characteristics. One example is the giant land tortoise, *Geochelone (Testudo) gigantea* Schweigger, on Aldabra Atoll (Gaymer 1968, Grubb 1971, Bourn & Coe 1978) which shows identical structural characteristics to those of the Arctic charr, but in an insular, terrestrial, tropical setting. Recently, a comparable structure has been described for the orange roughy, *Hoplostethus atlanticus* Collett, in the deep waters off New Zealand (Gauldie *et al.* 1989). Griffiths (1994) also documents bimodality in 19 species of freshwater fish, with a systematic increase in the frequency with latitude.

This widespread phenomenon evidently has fundamental implications for the development of ecosystem structure. If a modal structure is to develop and be maintained indefinitely, individual growth must be variable resulting, as observed, in the modal length group being composed of fish of many ages. Behavioural effects may be at

least partly responsible, and evidence from other Arctic charr lakes (Johnson 1983) strongly suggests internal regulation of growth and recruitment. This is supported by Healey's (1980) conclusion, as a result of the experimental exploitation of whitefish (*Coregonus clupeaformis* (Mitchell)) in northern lakes, that recruitment and growth of young fish is regulated by the established population of mature fish.

In a wider context, it has been shown experimentally that Arctic charr populations exhibit a high degree of inertia to change, and that there is a well-damped return to the original configuration following severe disturbance (Johnson 1983, 1994). This evident stability of Arctic fish populations is in strong contrast to the fluctuating nature of the small mammal populations of the surrounding tundra (Elton 1924, 1927, MacArthur 1955). A number of workers over many years have speculated as to the reasons. Tansley (1935), for example, concluded: "The more relatively separate and autonomous the system, the more highly integrated it is and the greater the stability of its dynamic equilibrium". Johnson (1981, 1983) concludes that this is due to the "highly autonomous nature of the system combined with internal damping, where internal damping is due to the "top-down" effects imposed by the terminal species in the food-chain (Northcote 1988)". This phenomenon deserves closer attention (Chapter 6).

2.5.3 Ecological segregation

Field observations in the Borup lakes strongly suggest that different, semi-discrete habitats exist within lakes with the nature of these habitats changing over the seasons,

each habitat supporting an optimal size of fish characterised by the modal value of the appropriate morph. The absence of other fish species capable of surviving at these latitudes allows the different modal sizes of charr, with their different morphological characteristics, to occupy specific "niches" which, in a more clement system, would be occupied by distinct species. Reproduction, when it occurs, occurs at an optimal size, specific to the niche, at which most energy is available to meet the demands of spawning. The occupancy of a given habitat is based on agonistic hierarchical relationships by which the smaller fish are excluded by the larger ones from the preferred habitat. A limitation of this work is that practical considerations precluded determination of the degree of habitat segregation during late-August to May.

2.5.4 Reproduction

A most important feature of these unexploited populations at the northernmost extreme of land is that reproductive individuals were caught within all size modes sampled and that lifetime energetic investment in reproduction was extremely low. This low level of surplus energy is entirely consistent with the findings of Venne & Magnan (1989) who examined the variation of the main life history parameters of Arctic char along a north-south gradient. Growth rate and relative fecundity were found to decrease with increasing latitude; but longevity, age at maturity and relative egg diameter increased. The Borup data fit these trends well, with the exceptions that the population age classes never reached the stage where 50% spawned in any one year and relative egg diameter was lower than further south (Sectionn 2.4.9). Whilst it is possible that the readings for relative egg size are due to the measurements being taken early in the growing season,

both observations are nevertheless consistent with a picture of decreasing available energy with latitude.

The regression of gonad weight relative to body weight (GSI), against length of mature female spawners from all lakes combined (Figure 2.9), shows a smooth progression from fish of 100 mm to fish of 400 mm. This progression indicates an ability to spawn at all sizes above the minimum sampled (100 mm), although in the prevailing conditions certain specific sizes are favoured. At the same time, there is a progression with respect to other characteristics: the 100 mm fish exhibit obvious juvenile characteristics such as parr-markings, small mouths and small eyes while those in the 400 to 500 mm length-class are similar to the anadromous or sea-run adult charr of many northern systems, having silvery coloration, large eyes and a large mouth with many backward-sloping teeth.

2.5.5 Life history

Life histories are difficult to work out when there are two morphs of the same species, each with reproducing individuals, each exhibiting what are usually regarded as juvenile characteristics. Thus, the juveniles of one morph are indistinguishable from the adults of the other. This condition, the attainment of reproductive status whilst retaining ancestral juvenile characteristics, is referred to as paedomorphosis (Gould 1977).

Life history theory, according to Wootton (1985), attempts to predict which life history patterns will be appropriate in particular environments, on the assumption that there is a

trade-off between present reproduction and later expected reproduction. If mortality is high over the average life span, then it is advantageous to have high reproductive output now, since later opportunities will be small. When mortality rates are low and, as in most fish, growth is indeterminate and fecundity increases with body size, it may be advantageous to delay reproduction for as long as practicable, because of the reduction in growth caused by reproduction.

The greatest point of interest in this study is that more than one successful life history pattern can apparently coexist within the same lake, with Dwarfs and Normals representing alternatives. The life history patterns represent alternatives because it appears that the heavy energetic cost of early reproduction for Dwarfs may inhibit the rapid somatic growth necessary for recruitment to the Normal size class. Similarly, differences in size and diet between lakes implies subtle variations in life history strategies on an allopatric basis. The remainder of the thesis concentrates on how such alternative life history strategies might be maintained and on their ecological significance.

3. Charr Parasites and Planktonic Intermediate Hosts

Parasite Fieldwork

Supervised by Professor Clive Kennedy

3.1 Chapter Abstract

Three species of tapeworm, *Eubothrium salvelini*, *Proteocephalus* spp. and *Diphyllobothrium ditremum*, were found in charr from the Borup lakes as well as the parasitic free-swimming copepod *Salmincola edwardsii*. The parasite fauna are thus similar to those of other High Arctic Islands in Canada and Europe (e.g. Kennedy 1978 a,b); and the presence of the tapeworms implies that feeding upon copepods and/or fish is a more important part of the charr diet than would be suspected from the data in Chapter 2. A high degree of over-dispersion (or variation) is apparent in the distribution of the number of parasites per host and this is interpreted as an indicator of heterogeneity in transmission to individual charr. This heterogeneity translates in ecological terms to individual specialisation in feeding tactics within the population and this, once more, contradicts the evidence of Chapter 2. The distribution of *D. ditremum* in the bimodal populations of Lakes C and H is examined in detail. High levels of infestation are apparent in a few of the largest individuals and one interpretation is that this is a result of feeding specialisation as a cannibal. It is possible that parasite-induced host mortality may be occurring amongst these highly infected individuals but this is not proved.

3.2 Introduction

Despite ecosystem simplicity and the sampling period covering much of the growing season, the short summer survey of Chapter 2 could only provide a limited ecological perspective. Identified limitations were that fish of less than approximately 10 cm were not sampled, nor was a suspected planktonivorous mode in Lake H (Section 4.3). In dimensions of time, neither spawning nor the winter season were covered; and, with individuals living for up to 25+ years, the results of fieldwork from two summers can only be seen as a snapshot. It is therefore necessary to glean information from as many sources as possible.

The use of parasites as biological tags is one means by which additional information about host biology may be obtained. This has been used both in assessing the movement and origin of stocks (e.g. Groot *et al.* 1989, Dick & Belosevic 1981, Bower & Margolis 1991) and in determining local feeding strategies (e.g. Henricsson & Nyman 1976, Walker *et al.* 1988). The main aim of this chapter is to take the latter of these potential uses of biological tags and to examine the distribution of parasites within the population. From this, subject to certain qualifications, parasites might give additional insight into charr feeding strategies and mortality. Information of specialist interest to the parasitologist is also gained and recorded at sections 3.4.2, 3.5.1 and 3.5.2; which are otherwise of secondary importance to the overall argument of the thesis.

3.2.1 Stochastic processes - summary of theory

Fundamentally, the distribution of parasites within a host population is a dynamic consequence of the transmission of the parasite around its life cycle. This is because the rate of increase of parasites in a host is equal to the rate of arrival of parasites minus the rate of departure (Anderson & Gordon 1982); and, over time, this will result in an infrapopulation of parasites within the individual. "Arrivals" are either immigrants (usually due to feeding), or juveniles born to adult parasites within the host. "Departures" are represented either by emigrants, or by deaths of parasites within the hosts.

Typically, infrapopulations of parasites are subject to a high degree of dispersion or variance and Anderson & Gordon (1982) use a stochastic model to analyse its cause. [3] In practical biologist's terminology, Anderson & Gordon's results indicate that the following factors will tend to result in under-dispersion ($s^2/\bar{x} < 1$):-

1a. Parasite mortality within the host, especially if density-dependent.

1b. Negative density-dependent processes (meaning that the more parasites within the host, the fewer extra parasites can become established within the host).

1c. Parasite-induced host mortality (meaning host death rate positively correlated with parasite burden).

[3] Dispersion is usually defined either as the variance divided by the mean ($s^2/\bar{x}$), or as the parameter k of the negative binomial distribution.

Similarly, over-dispersion($s^2/\bar{x} > 1$) is generated by:-

2a Heterogeneity in host susceptibility to infection.

2b Heterogeneity in the ability of hosts to kill parasites whether by immunological or other response.

2c Direct reproduction in the host.

3.2.2 Parasite life cycles

The distribution of different parasites within a given host population varies with the parasite species owing to their different life cycles. Figure 3.1 is an illustration of that for *Diphyllobothrium ditremum,* a cestode parasite regularly found in Borup charr as plerocercoids within cysts on the stomach wall. An example of a heavily infested individual is photographed at Figure 3.2. The usual definitive hosts for *D. ditremum* are considered to be ducks and divers (*Gavia* sp.); and whilst divers were present at Borup, it has neither been proved nor disproved that the other bird species present such as the glaucous gull, *Larus glaucoides*, and Arctic terns, *Sterna paradisaea* Pontoppidan, could not also be hosts. The first intermediate host is known to be copepods, whilst charr are the second intermediate host.

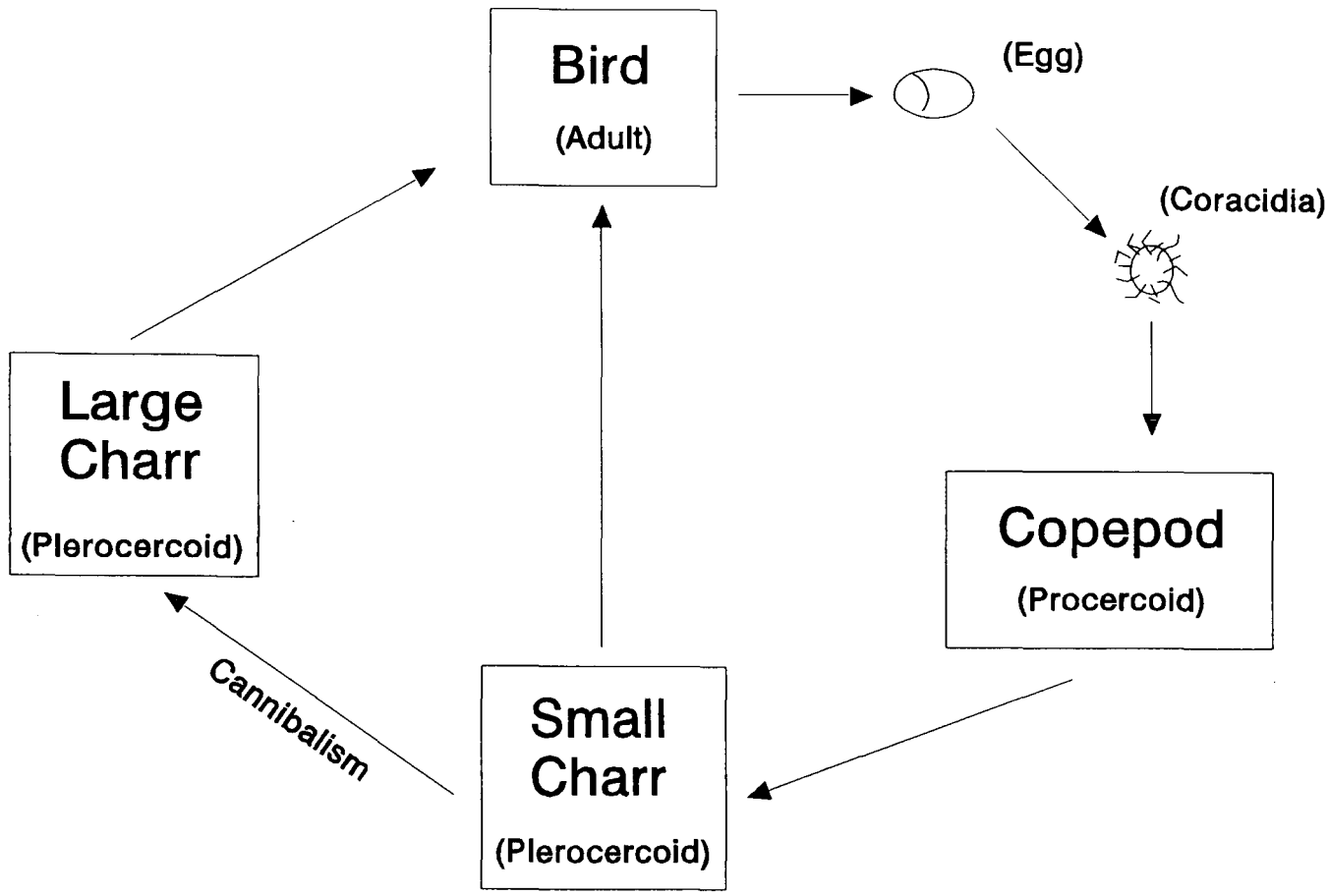


Figure 3.1 Schematic of the Diphyllobothrium ditremum life cycle in the Borup lakes. The definitive host is a bird, most probably a diver. Life cycle stages include free-living ciliated coracidia, procercoids in copepods and plerocercoids in charr. Plerocercoids can be transmitted from smaller fish to piscivorous charr (Curtis 1984).

Three other species of parasite were found in charr from the Borup lakes. *Salmincola edwardsii* is a parasitic copepod with free-swimming larvae and a direct life cycle which attaches itself to the gills and inner operculum of the charr. *Eubothrium salvelini* and *Proteocephalus* spp. are intestinal tapeworms which use charr as their final host, thus achieving their adult stages and reproduction within the fish. The intermediate host is, once again, copepods; but there is no evidence to suggest retransmission from fish to fish via cannibalism.

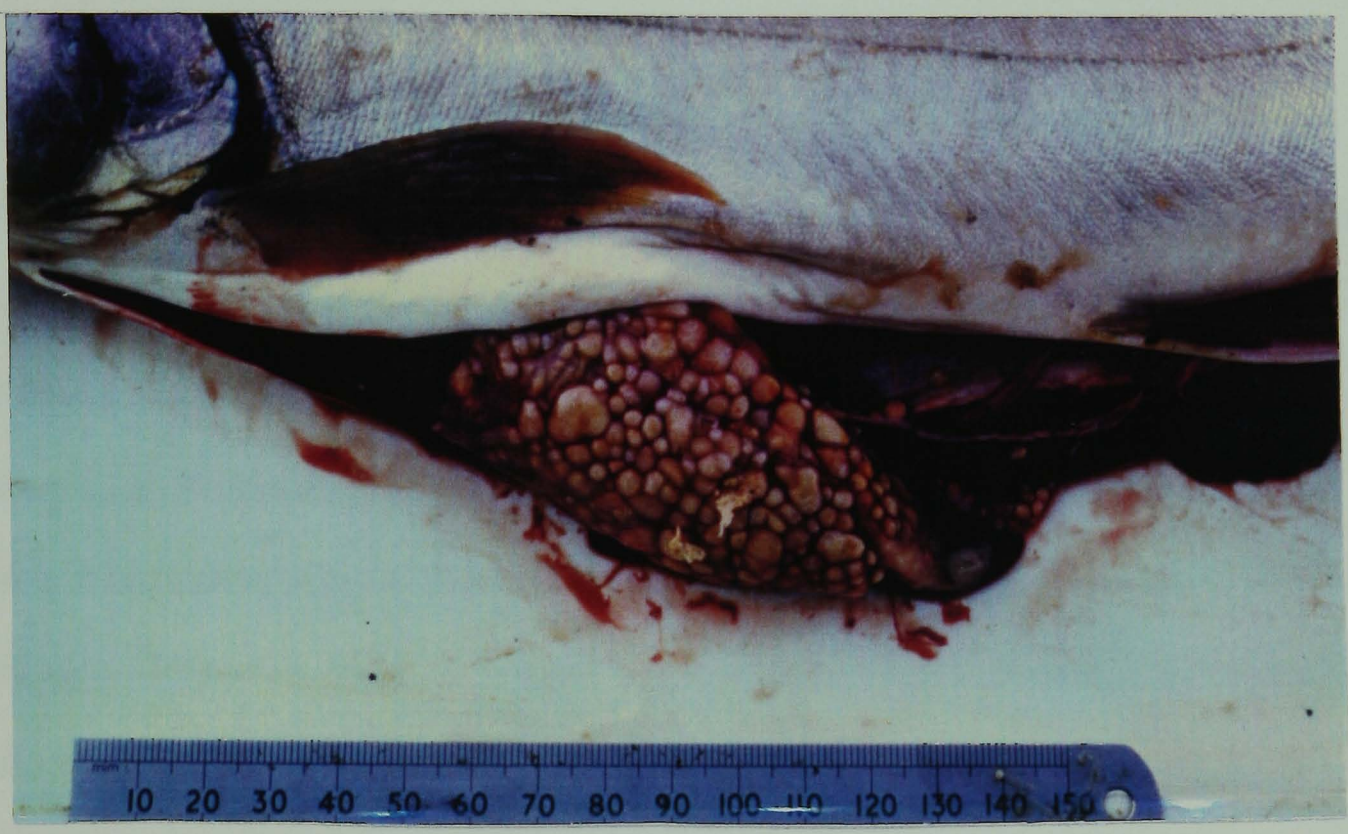


Figure 3.2 The stomach wall of a Normal charr from Lake H heavily infested with D. ditremum.

3.2.3 Stochastic processes and parasite life cycles

The *Diphyllobothrium* life cycle is highlighted because four of Anderson & Gordon's (1982) six dispersion factors are insignificant; and this simplification allows some potential to separate otherwise complex ecological processes. The key feature is that charr are a second intermediate rather than a final host and this means that there is no direct reproduction of the parasite within the host (2c).

Of the other factors leading to over-dispersion, heterogeneity in the ability of hosts to kill parasites (2b) is thought unlikely since the host strategy is to encyst the parasite and no empty cysts were found. Bylund (1972) also found that salmonids have a poorly developed resistance against the plerocercoids of *D. dendriticum*. Additionally, Halvorsen & Andersen (1984) report no indication of plerocercoid mortality on charr kept in a laboratory tank for three years, but this may not indicate much for Borup charr since ages of up to 24 years were observed. Using the same evidence, it is also possible to discount parasite mortality within the host (1a) as a significant factor towards under-dispersion.

Density-dependent processes (1b) are also thought negligible since heavily encysted hosts were comparatively rare meaning that the majority of the population harbour parasites well below the maximum observed level. This leaves heterogeneity in host susceptibility to infection (2a) as the key mechanism leading to over-dispersion; whilst parasite-induced host mortality (1c) leads to under-dispersion.

3.2.4 Uncertainties in parasite transmission rates

Despite the above arguments that the distribution of *D. ditremum* within the charr population should primarily be controlled by parasite-induced host mortality and heterogeneity in host susceptibility to infection, a number of uncertainties in transmission rates means that any conclusions on this basis must be qualified. For example, there is some controversy over whether *D. ditremum* can re-establish themselves in a large fish when its small fish host falls victim to piscivory. Halvorsen & Wissler (1973) failed to establish this in Rainbow trout, *Oncorhyncus mykiss*, but Curtis (1984) successfully demonstrated it in charr.

Uncertainties over the final host have already been discussed and are even greater when the transmission path via copepods is considered. In nature, the density of infected zooplankton is low (Pasternak *et al.* 1995), an infecting parasite may not develop, timing of transmission is critical, there is some specificity to host, and when an infected zooplankton is detected it is not usually possible to determine which species is infecting it (Henricsson 1978). Behavioural effects may also be important. Diaptomids, for example, are thought to escape the attention of fish predators by their means of locomotion (Lindström 1955, Brooks 1968). Similarly, Pasternak *et al.* (1995) showed that infected copepods had reduced motility and hence were likely to be more susceptible to predation. Overall there are many sources of uncertainty in the parasite-copepod interaction.

3.3 Materials and Methods

In a survey for potentially suitable intermediate hosts, both littoral and planktonic crustacea were searched for in the 1991 fieldwork. Zooplankton were sampled at regular intervals throughout July and August using both 500 μm and 100 μm mesh plankton nets hauled vertically through the water column. Early season sampling was conducted through holes in the ice, with later sampling being conducted by boat in Lake H and swimming in the smaller lakes. Samples were taken approximately in the middle of Lakes A,B and C; whilst Lake H was sampled at the head, middle and tail. Sampling was also divided by depth; one sample being taken over the whole water column and another over the top half only. Owing to a low density of zooplankton in some samplings, several vertical hauls were conducted without emptying the net in between on these occasions. Littoral crustacea were sampled in open water by using ca.4 m horizontal hauls at a depth of ca.1 m in the littoral zone. Samples were preserved in 2% formalin and counts of individuals by taxonomic class produced on return to UK. The relative density of zooplankton was calculated by dividing the number of individuals caught in a sample by the total distance the net had travelled. The arithmetic mean of all samples from a lake on a particular day was calculated and the result plotted against date. Identification to species level was later completed by Dr. Patalas from the Freshwater Institute in Winnipeg, Canada (Enclosure 5)

The parasite material used in this chapter was collected during the sampling of charr described in chapter 2. Charr were examined by standard techniques, and most major organs were searched for the presence of metazoan parasites. Protozoa were not

searched for, nor was the blood system examined. The numbers of individuals of each parasite species were determined for fish in Lakes A, B and C. Some fish in Lake H were very heavily infested and precise numbers were not determined in all cases. All identifications were confirmed on material brought back to England.

Whilst it would have been desirable to conduct individual counts of the high levels of *Diphyllobothrium* found in many Normal charr from Lake H, it was not practical to do so. Instead a semi-quantitative points method was introduced and calibrated against actual counts. The same worker allocated points in all cases, and it was intended that the scale should be approximately exponential. 43 points were used in this calibration and 77 points were estimated from it. Figure 3.3 illustrates a plot of individual counts against the points allocated. Results of linear regression on Figure 3.3 are tabulated in Table 3.1.

Points	Count estimate
0.5	11
1	20
1.5	36
2	65
2.5	117
3	210
3.5	380
4	685
4.5	1236
5	2229
5.5	4019
6	7248

Table 3.1 Results of linear regression on Figure 3.3. These estimates are used when full counts are not available in the calculations for Lake H.

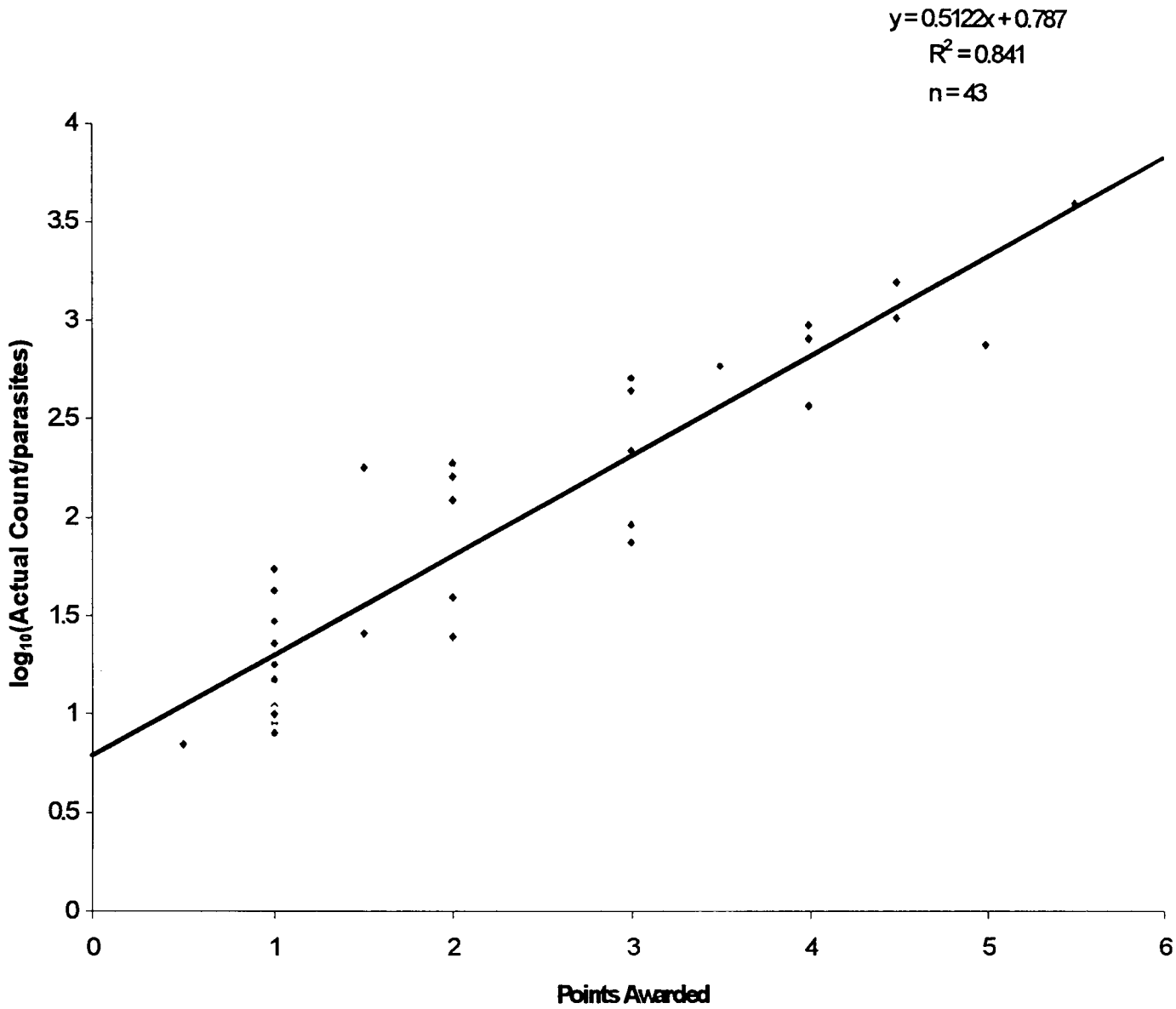


Figure 3.3 Calibration of the points method of estimation applied to 77 Normal charr from Lake H. The horizontal axis indicates the subjective points allocated to the parasite load of an individual, whilst the vertical axis is the actual count.

In order to gain information on potential variation in transmission rates and possible parasite-induced host mortality, the prevalence and abundance of infection by *D. ditremum* was plotted against length. For Lake H, these plots included data estimated using the points system. Age against prevalence/intensity plots were also produced but are not illustrated since they provide a broadly similar picture to the length data but with less sharply-defined changes between classes. This tentatively indicates both that length and age are at least loosely correlated but also that length is a better predictor of ecological niche than age (c.f. Chapter 2). Only data from Lakes C and H are used. 1988 data were used in Lake H, whilst 1988 and 1991 data were combined in Lake C to augment sample size. The "Dwarfs-only" Lake A effectively only had one length class so there was no means of detecting a trend, whilst Lake B only yielded three Normals leaving insufficient data for analysis.

Dispersion of the *Diphyllobothrium* infrapopulations was also calculated against length for Lakes C and H in order to gain some idea of the degree of aggregation of the parasites. Dispersion was calculated as the ratio of the variance to the mean ($s^2/\bar{x}$). The terms "prevalence", "abundance", "intensity" and "infrapopulation" are used according to their standard definitions in Margolis *et al.* (1982).

Statistical handling of the *D.ditremum* data was achieved by ordering the fish by length and then splitting them into sub-samples of 20 fish (Lake H) or 10 fish (Lake C). Adjacent pairs of these groups were then amalgamated and the prevalence, abundance, average length and dispersion calculated for each overlapping class of 40 fish (Lake H) or 20 fish (Lake C). Average length for each set of data was then used on the graph x-

axis, with the other values separately plotted against suitable scales. Data from 75 individuals were used in Lake C and 242 in Lake H.

3.4 Results

3.4.1 Crustacean surveys

The surveys using plankton nets revealed major differences between the lakes. Midwater sampling in Lake H using the 500 μm mesh net invariably caught the calanoid copepod, *Limnocalanus macrurus* Marsh, no other species were found. In contrast, sampling with this size of net met with little success in Lakes A,B & C, although some plankton were taken, confirming the suggestion that only one planktonic species was present in Lake H (Figure 3.4).

In Lake H, midwater sampling with the 100 μm mesh net met with little success indicating, presumably, that *Limnocalanus macrurus* is capable of evading capture because of a pressure wave "build-up" in advance of such a fine-meshed net and that other species were absent. In Lakes A,B and C, mixed populations of Copepods, Cladocera and Rotifers were caught, but in different quantities (Figure 3.5). *Limnocalanus macrurus* Marsh, the cyclopid copepod *Cyclops scutifer* (Sars), and the cladocera *Daphnia middendorffiana* Fischer and *Bosmina longirostris* (O.F. Mueller) were identified at the geographical locations specified in Table 3.2.

	Daphnia middendorffiana Fischer	*Bosmina longirostris* O.F.Mueller	*Cyclops scutifer* Sars	*Limnocalanus macrurus* Marsh
Lake A	X		X	(X)
Lake B	X	X	X	(X)
Lake C	X	X	X	
Lake H				X

Table 3.2 Planktonic crustacean species identified from Lakes A, B, C and H. The brackets indicate that *Limnocalanus marurus* *Marsh was found in only small quantities in Lakes A and B.*

A marked seasonality was apparent in all samples, with a dramatic increase in zooplankton abundance occurring about iceout[4]. Local climatic variations and differences in the thermal capacity of the lakes led to some variation in the date of iceout, which is marked on the graphs. Iceout appears a much more relevant time datum with respect to general biological activity than calendar date and probably corresponds to a spring phytoplankton bloom as light, nutrient and temperature regimes reach optimum conditions.

[4] "Iceout" occurs when all the lakeice is melted for the first time in a season.

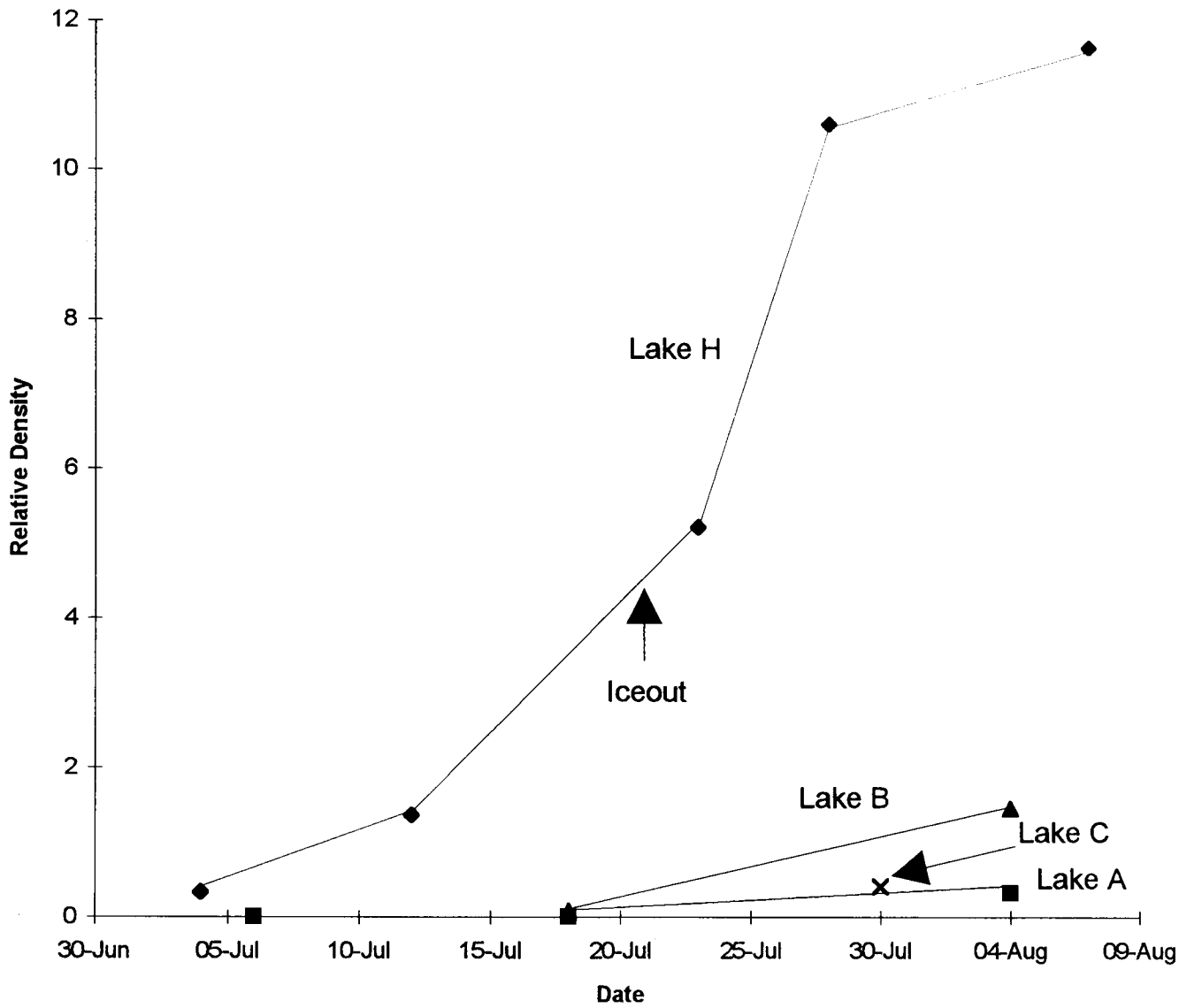


Figure 3.4 The relative density of zooplankton caught in the coarse, 500 μm mesh, plankton net against time. The results from Lake H indicated a monoculture of the copepod Limnocalanus macrurus Marsh which increased markedly at iceout. The other lakes contained only small quantities of zooplankton which were sufficiently large to be trapped by this mesh.

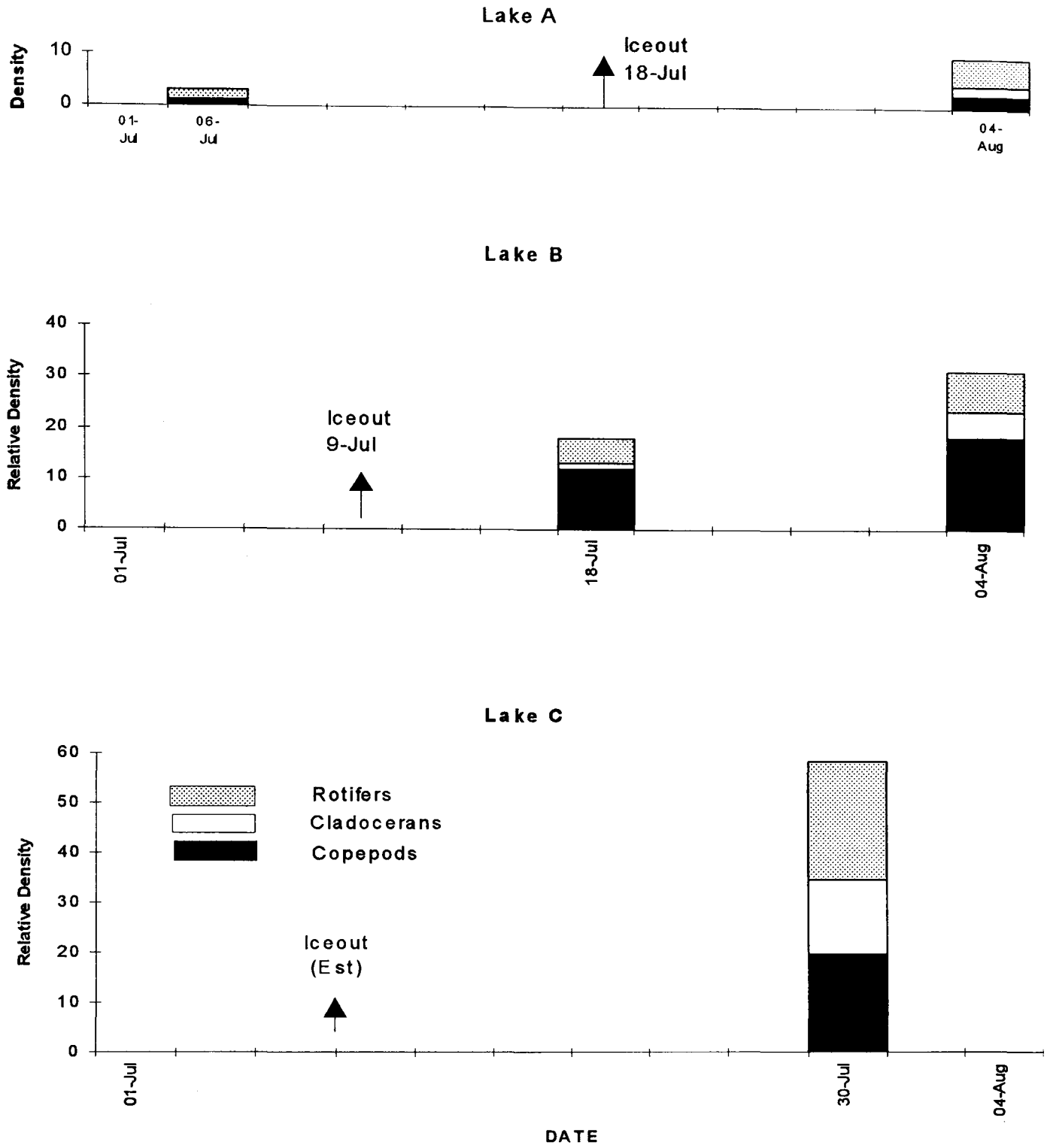


Figure 3.5 The relative density of zooplankton caught in Lakes A, B, C when using the fine, 100 μm mesh, net. Little success was achieved in Lake H, presumably because Limnocalanus macrurus is able to evade such a net. The graphs are plotted to the same scales, with date on the horizontal axis. Despite a limited number of data points, it is apparent that density increases rapidly around iceout and the lakes support quantitatively different densities of zooplankton.

In the littoral zone, *Chydorus sphaericus* (O.F. Mueller), *Eucyclops agilis* (Koch) and *Macrocyclops magnus* (Marsh) were variously identified in the different lakes. In Lakes B and C, the littoral zone was heavily vegetated and extended throughout the entire lake. Lakes A and H hardly had any littoral zone at all, meaning that littoral crustacea probably formed a negligible proportion of the charr diet. The results of the identifications are summarised in Table 3.3. No attempt was made to identify the rotifers.

	Chydorus sphaericus O.F.Mueller	*Eucyclops agilis* Koch	*Macrocyclops magnus* Marsh
Lake A		X	
Lake B	X	X	X
Lake C			
Lake H	X	X	

Table 3.3 Non-planktonic crustacea caught in the littoral zones of Lakes A, B, C and H. This is likely to be an incomplete list owing to the difficulties of systematic survey in the littoral zone.

3.4.2 Parasites

3.4.2.1 ***Inter-lake comparison by species.*** *(from Enclosure 2)*

Parasite infection levels differed considerably from lake to lake (Table 3.4). Two species were found in all four lakes (*D. ditremum* and *Proteocephalus*) and only these two in Lake A. Lake B contained *E. salvelini* in addition. The prevalence and intensity of each species also varied from lake to lake. *S. edwardsii* was most abundant and prevalent in Lake H. *D. ditremum* was least common in Lake B, was more common in Lake C and dominated Lake A, but reached its maximum abundance in Lake H where one fish harboured just over 4000 individuals. Levels of *Proteocephalus* were comparable in Lakes A, B and C but this species was rare in Lake H where, by contrast, *E. salvelini* was the commonest and most abundant intestinal tapeworm. With the exception of *Proteocephalus*, therefore, all species were most prevalent and abundant in Lake H. Identification of *Diphyllobothrium* follows current opinion, but identification of proteocephalid tapeworms is both difficult and uncertain. The material was probably *P. tumidocollus*.

	Lake A	Lake B	Lake C	Lake H
No. of fish examined	32	26	57	60
% of fish infected	81.2	65.4	57.9	86.7
Salmincola edwardsii				
Prevalence	-	-	5.3	18.3
Mean(max.) intensity	-	-	1(1)	11.7(51)
Diphyllobothrium ditremum				
Prevalence	75.0	21.1	24.6	75.0
Mean(max.) intensity	13.6(75)	1.7(3)	10.1(84)	300.00(4242)
Proteocephalus sp.				
Prevalence	53	42.3	33.3	1.7
Mean(max.) intensity	9.0(48)	9.5(32)	10.6(48)	1.0(1)
Eubothrium salvelini				
Prevalence	-	34.7	12.3	43.3
Mean(max.) intensity	-	1.3(2)	1.6(3)	3.4(20)

Table 3.4 Level of parasitic infestation of Arctic charr from Lakes A, B, C and H (prevalence = % of fish infected; intensity = no. of parasites per fish of those infected). Intensity data refer only to the subsample of fish for which all parasite numbers were counted in the 1988 fieldwork. Estimates using the points method for D. ditremum in Lake H are not included.

3.4.2.2 *Prevalence and Abundance against Length. Lakes C and H*

Plots of prevalence and abundance of *D. ditremum* infection against length of fish from Lakes C and H are shown in Figures 3.6 and 3.7. The length-frequency histogram for the charr from each lake is included beneath. The Lake H graph includes data estimated using the points method (Section 3.3). Abundance is nearly two orders of magnitude different between lakes (c.f. Intensity values in Table 3.3), but both lakes share the common feature of a sharp increase coinciding with the peak of the larger size mode. Prevalence of infection rises steadily to 100% in Lake H, but shows a similar pattern to abundance in Lake C.

3.4.2.3 *Dispersion against Length. Lakes C and H*

Figures 3.8 and 3.9 show plots of dispersion ($s^2/\bar{x}$) against length in the distribution of *D. ditremum* infection amongst individuals from Lakes C and H. Each data point on the graphs corresponds to those in the prevalence/abundance plots. Levels of dispersion are different between the lakes. Lake C shows a similar "L-shape" graph to its prevalence and abundance data. Lake H shows a more complex pattern: a rise in dispersion with length in between the two charr size modes, followed by a steep rise corresponding with the peak of the larger size mode, and a subsequent drop.

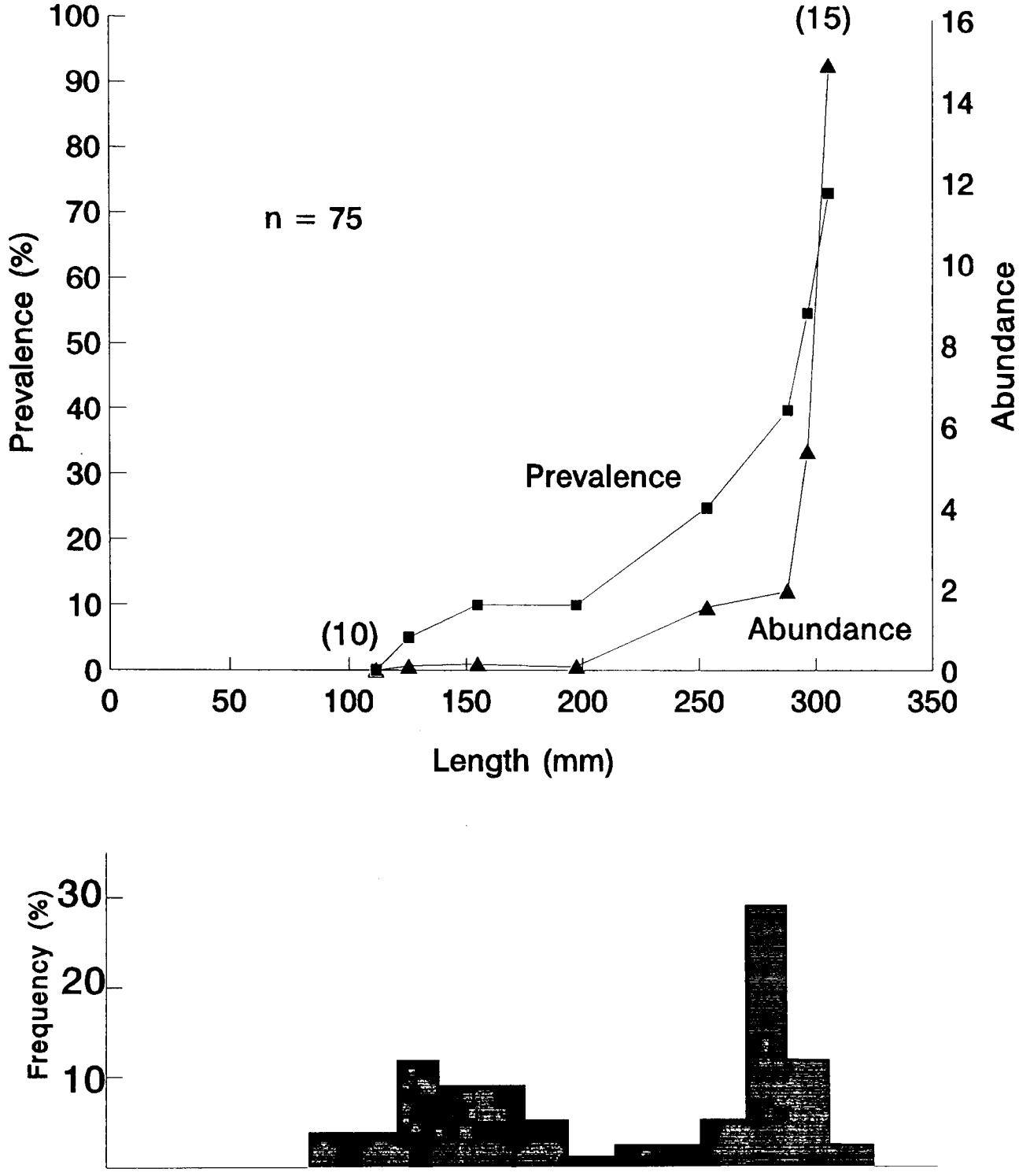


Figure 3.6 Prevalence and abundance of D. ditremum infestation against length of charr in Lake C. The length-frequency histogram for the fish is beneath. The sample size of each point is 20 unless a smaller number is indicated in brackets.

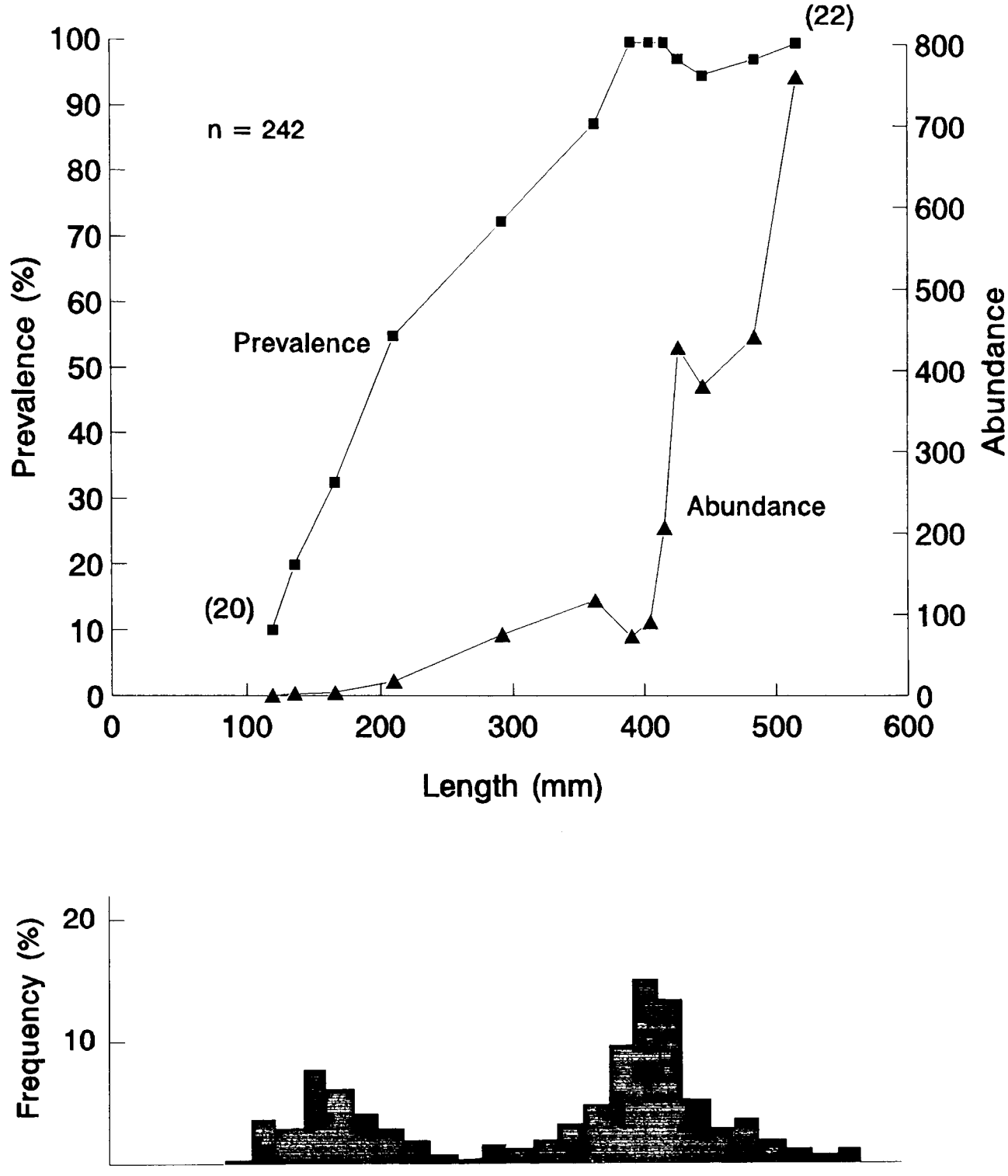


Figure 3.7 Prevalence and abundance of D. ditremum infestation against length of charr in Lake H. The length-frequency histogram for the fish is beneath. The sample size of each point is 40 unless a smaller number is indicated in brackets.

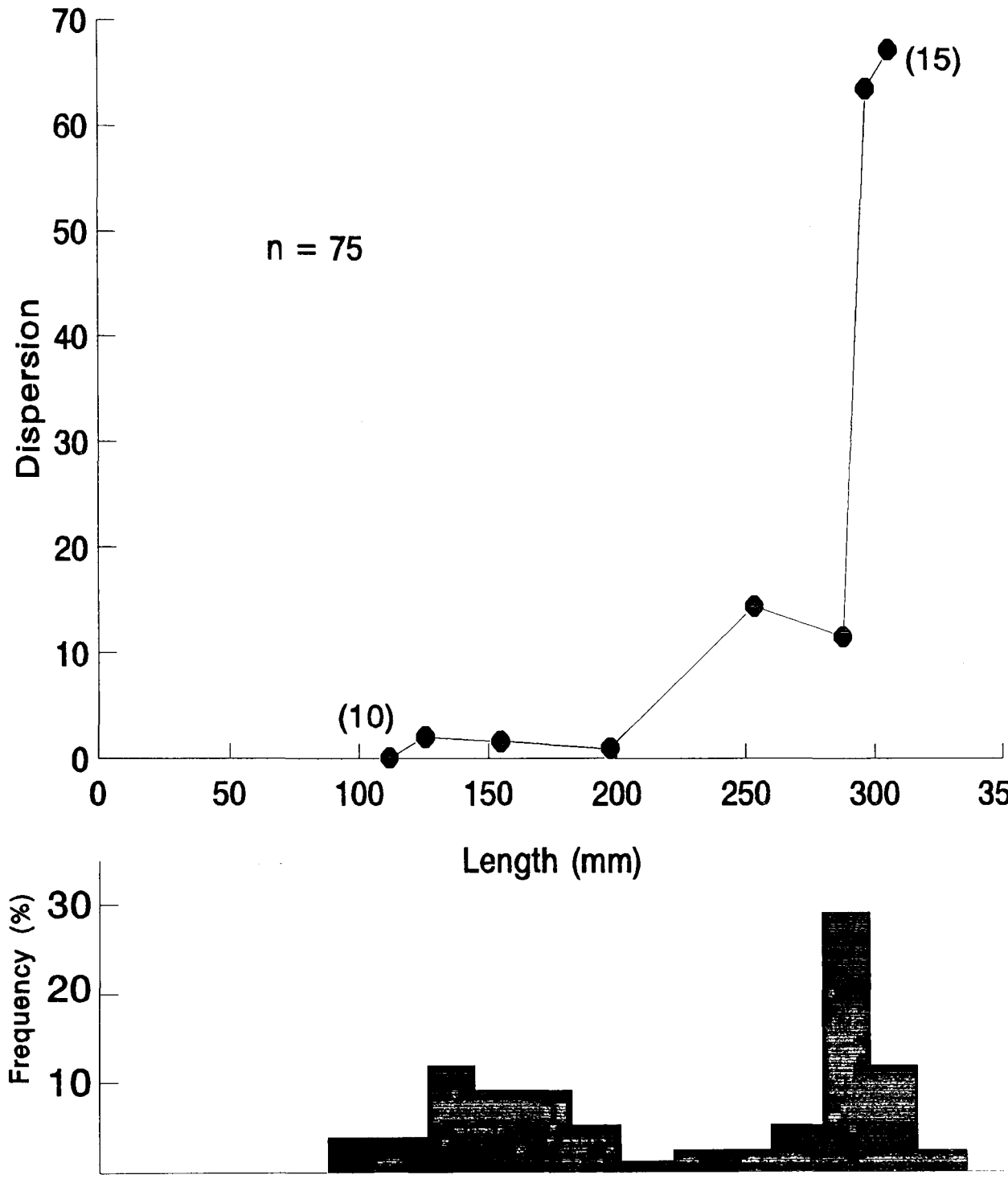


Figure 3.8 Dispersion of <u>D. ditremum</u> in Lake C as a function of length. The length-frequency histogram for the fish is beneath. Dispersion is calculated as $s^2 / \bar{x}$, using the same samples as for the abundance/prevalence plots.

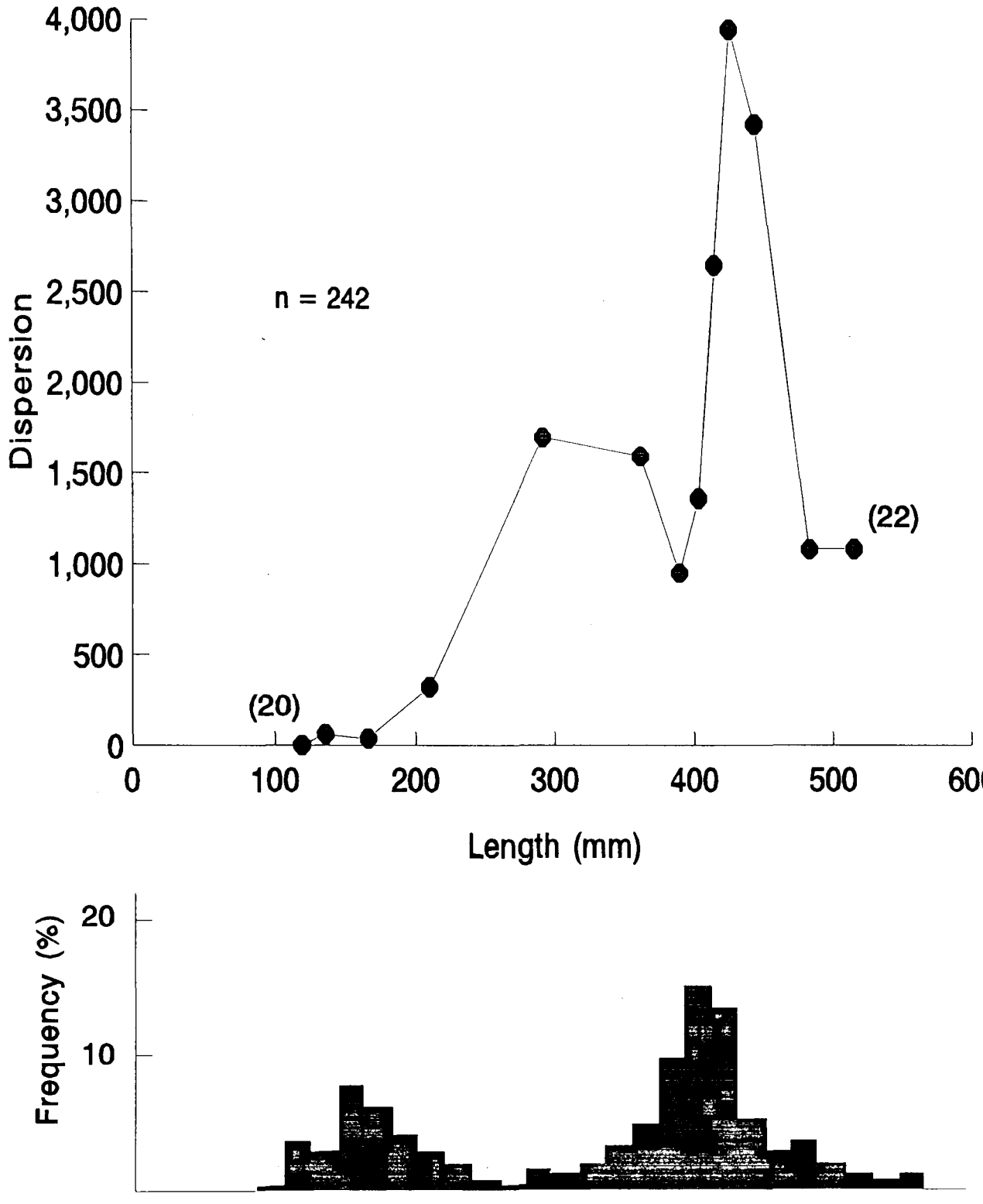


Figure 3.9 Dispersion of <u>*D. ditremum*</u> *in Lake H as a function of length. The length-frequency histogram for the fish is beneath. Dispersion is calculated as* $s^2 / \bar{x}$, *using the same samples as for the abundance/prevalence plots.*

3.4.2.4 Individual intensity against length. Lake H.

The introduction argued that parasite-induced host mortality is the key feature in reducing dispersion, with heterogeneity in host susceptibility to infection acting to increase it. Determining which is the predominant process requires inspection of the raw data and Figure 3.10 shows this for Lake H. As charr from Lake H increase in size beyond 400 mm the minimum levels of infection increase to approximately 1000 parasites per fish. This is interpreted as indicating a reduction in feeding heterogeneity since lightly-infected individuals are lost. Simultaneously, the maximum infection levels fall to approximately the same level and this may indicate parasite-induced host mortality. The figure is annotated with this interpretation and suggests that a reduction in heterogeneity in host susceptibility to infection and parasite-induced host mortality may, in fact, both be increasingly important as host size increases. Another interpretation, which is theoretically possible but is not supported by observation on fish diet, is that there are no new infections in older fish and this is followed by their natural death.

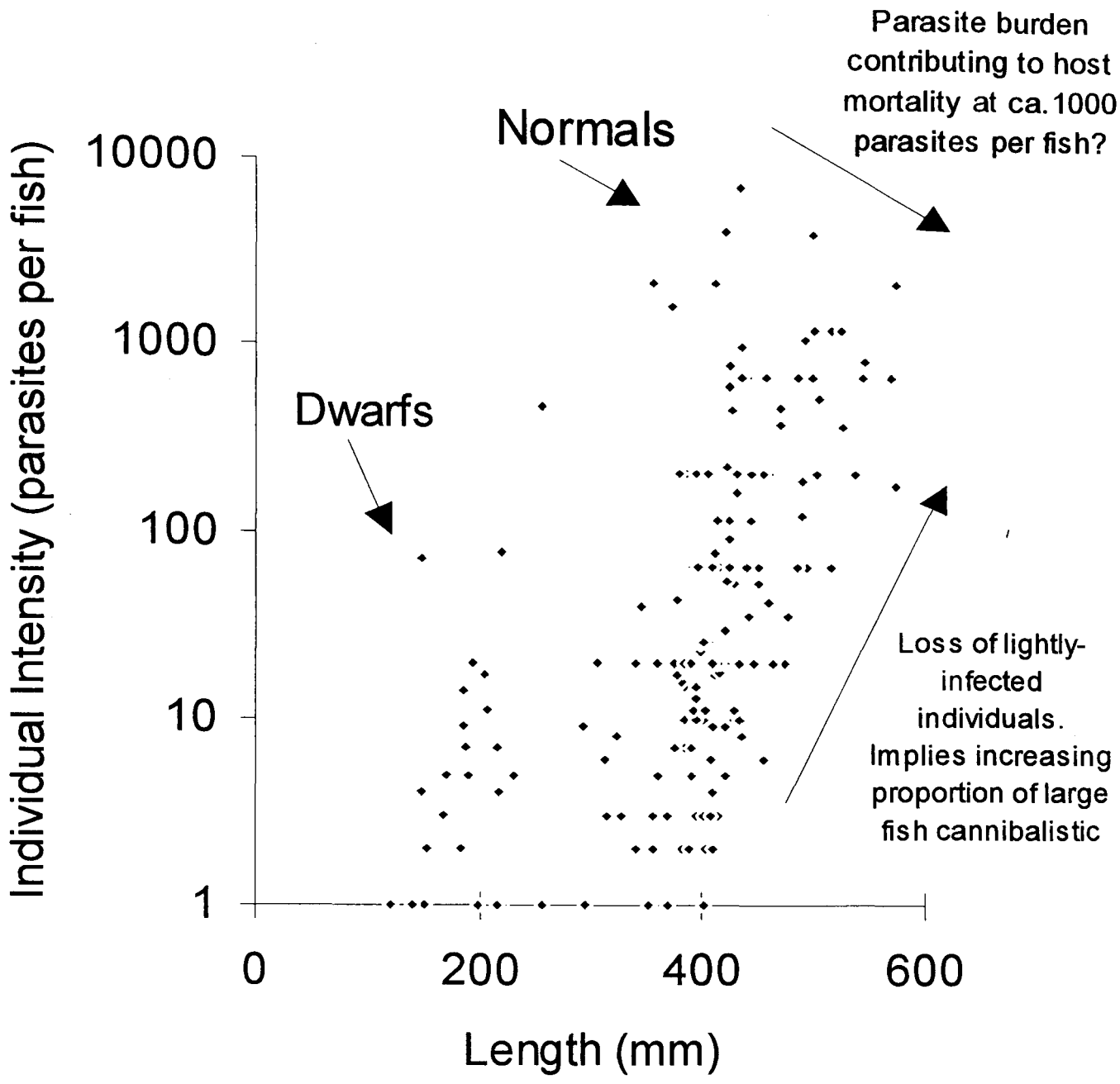


Figure 3.10 Individual intensity of infestation against individual length for Lake H. Note that the logarithmic scale means that zero infestations are not shown; and also that the figure includes data estimated using the points method. The plot is annotated to indicate the reducing heterogeneity in susceptibility to infection at the larger lengths and the simultaneous possibility of parasite-induced host mortality. Other interpretations are theoretically possible such as no new infections in older fish accompanied by their natural death.

3.5 Discussion

3.5.1 Comparison with other studies

All four species of parasite have been recorded from charr in other locations in the Arctic, and they, or their European equivalent, from charr in Europe (Dogiel & Markov 1937, Powell 1966, Konovalov 1975, Henricsson 1977, 1978, Beverley-Burton 1978, Conneely & McCarthy 1984, Curtis 1984, Halvorsen & Andersen 1984, Bérubé & Curtis 1986, Kristoffersen 1986, Due & Curtis 1995). The general characteristics of the parasite fauna of charr from Ellesmere Island are fairly similar to those on Bear Island in the Norwegian Arctic (Kennedy 1978 a,b). There, an additional species of nematode was present, but otherwise the same four species and with all four in increased abundance in the largest lake. On Bear Island also the fauna tended to be dominated by *D. ditremum*. Most lakes on the mainland have a slightly richer parasite fauna as species of flukes and nematodes may also be present. The above leads to the conclusion that the parasite fauna of charr in the High Arctic islands of Canada and Europe are similar.

3.5.2 Observations based on prevalence and intensity of parasite species in the Borup Lakes

Some inferences of ecological significance can be gained from the prevalence and intensity data that was presented in Table 3.4:-

1. The main feature of significance to host biology is that the parasite fauna are limited to those species having a planktonic larval stage or utilising planktonic intermediate hosts. This indicates that charr feed on zooplankton/fish even though this was not seen in significant numbers in the survey of Chapter 2. The reasons for this discrepancy are either that charr feed intensively on fish/zooplankton outside of the sampling period or that zooplankton disintegrate rapidly within the stomach and are hence underrepresented in samples (Henricson 1977; Kennedy *et al.* 1992). Seasonal variation in plankton feeding has previously been documented in other studies undertaken year round (e.g. Henricsson 1978, Bérubé & Curtis 1986).

2. The lack of *Salmincola edwardsii* in Lakes A and B, and *Eubothrium salvelini* in Lake A emphasises the importance of ecological history. Neither of these parasites have the advantage of an airborne definitive host and thus may not have reached the lake, or may not have re-established themselves after extinction.

3. The low prevalence and intensity of *Proteocephalus* spp. infestation in Lake H may indicate that a good intermediate host is lacking. If this is the case then *Limnocalanus macrurus* is unlikely to be an efficient intermediate host.

4. By contrast, the high intensity of *Diphyllobothrium* infection in Lake H implies that the calanoid copepod *Limnocalanus macrurus* is a suitable intermediate host. This is unusual since it is generally supposed that transmission of *Diphyllobothrium* via calanoid copepods is insignificant and that cyclopids are primarily responsible (e.g. Henricsson 1978). In Lake H, however, the contribution of littoral cyclopids is thought to be negligible since the density of the littoral cyclopid *Eucyclops agilis* (Koch) was low and the littoral zone only covers a small area of the lake. It is also considered unlikely that an undetected planktonic cyclopid was present since the prime candidate, *Cyclops scutifer*, was found using identical methods in the other lakes. It is thus concluded that there is no alternative method of transmission. It has, however, never been proved that transmission via Calanoida is impossible and it was indeed concluded by Guttowa (1961) for *D. latum* that Calanoida are more susceptible to invasion than Cyclopids. It may, therefore, be supposed that the usual limitation on parasite transmission via Calanoida is more due to their locomotive abilities and hence avoidance of predation than their susceptibility to infection.

5. The high prevalence of *Diphyllobothrium ditremum* in Lake A may be an example of how an interaction between intermediate and definitive hosts may be effecting the parasite density. In Lake A there was a high density of Dwarf fish with no Normals and it was also observed subjectively that this lake experienced more fishing pressure by predatory birds than the others. The interaction between a high density of prey-sized fish in a classic "stunted" population and a high prevalence of predation upon them may be leading to increased numbers of free-living *Diphyllobothrium* coracidia in the lake. A further factor may be that observed by Bérébé & Curtis (1986) in that poor feeding conditions may force charr to feed on copepods in the autumn at a time when no other food is available. This hypothesis is supported by the sparsity of the littoral habitat in Lake A.

6. The intensity of *Diphyllobothrium* infection in Lake H is over an order of magnitude higher than elsewhere. This may be due to the major difference in the probable intermediate host (*Limnocalanus* vs. *Cyclops*). An alternative hypothesis is that Lake H provides a larger relative volume of planktonic habitat than the other, smaller, lakes and hence that more charr feed planktonivorously.

3.5.3 Effect of approximations and sample size on parasite distribution analysis

The graphs of length against prevalence, abundance and dispersion for Lake H (Figures 3.7 and 3.9) include data estimated using the points method. There is an inevitable inaccuracy generated by use of this measure but, due to the properties of elementary statistics, insufficient to change materially the interpretation of the data. The reasons for this are that, for prevalence, the data are not affected at all; whilst, for abundance, every underestimate is statistically likely to be cancelled by an overestimate. The dispersion data are only slightly affected since the data at each extreme of the sample contribute far more to the variance value than small discrepancies in the middle of the sample range. The situation is further mitigated by the fact that data were only estimated for Normals and smaller fish were subjected to a full count. Ultimately, the analysis is much less affected by using the approximation technique than by excluding individuals altogether.

The issue of sample size is frequently controversial in this type of analysis as is the manner of dividing the population into samples. The method used achieves a degree of curve smoothing and also demonstrates that the observed patterns are not a result of one particular grouping of the data. Fair and equal sample sizes are also gained. The disadvantage is that data from each fish is used in two adjacent samples and thus that the plotted points are not independent of each other. In order to appreciate the results with each data point being independent of its adjacent points, the reader should ignore every other point plotted in Figures 3.6, 3.7, 3.8 and 3.9.

3.5.4 Size-specific changes in infection rate

The length against prevalence and abundance graphs for Lakes C and H (Figures 3.6, 3.7) indicate size-specific changes in average infection with length and, initially, it would seem entirely justified to claim good evidence for a general diet shift associated with the large size mode in both Lakes. Figures 3.8 and 3.9, however, indicate that variance is high so general conclusions based on averages may be misleading. In particular some quite large fish (Figure 3.10) have low levels of infection.

3.5.5 Heterogeneity in parasite transmission

The high variance of the distributions in Lakes C and H should not merely be interpreted as noise in the data. Instead, the stochastic theory of Anderson & Gordon (1982) argues that it indicates heterogeneity in host susceptibility to infection over all fish sizes. Predominantly, this heterogeneity would arise from individual differences in feeding habits within all size classes. This contradicts the evidence of Chapter 2 where fish of the different size classes appeared to have a similar diet within their separate habitats.

Given that accumulation of *D. ditremum* can only occur as a result of feeding upon copepods and/or another (planktonivorous) fish, this heterogeneity is interpreted as meaning that some individuals in both size modes specialise on these two food types.

Some small charr probably plankton feed, whilst some of the larger charr are also piscivorous.

3.5.6 Parasite-induced host mortality

The drop in dispersion for the large size classes in Lake H (Figure 3.9) requires explanation. One explanation is that it might be a statistical anomaly and Anderson & Gordon (1982) show that "bizarre patterns" can be a result of small sample size. This can be discounted in Lake H since the sample sizes are respectable (usually 40, with a minimum of 20). The issue of small sample size is, however, relevant to Lake C (Figure 3.8) where, if the final sample uses the largest 11 fish rather than the largest 15 fish, an apparently similar drop in dispersion is gained (not illustrated). It is, thus, concluded that the drop in dispersion is a genuine feature of Lake H and it may also occur in Lake C, but in this case the sample size is too small to prove it.

From Section 3.2.1, the primary factor tending towards under-dispersion is parasite-induced host mortality. However, this must be qualified since a reduction in the degree of heterogeneity in the infection rate may also contribute to the same symptoms. This reduction in heterogeneity could occur as a result of an increasing proportion of the largest fish in the population adopting the same feeding strategy as they grow larger. Increasingly cannibalistic tendencies with length is a possible mechanism. Figure 3.10 is annotated with the suggestion that both parasite-induced host mortality and reduced

heterogeneity to infection are occurring simultaneously. Figure 3.10 could, however, also be interpreted as showing no new infections in old fish accompanied by their natural death. The mechanisms involved in the, apparently genuine, reduction in dispersion are thus not conclusive, inferring that parasite-induced host mortality is likely to make some contribution to mortality rates in the largest size classes but this can neither be confirmed nor quantified.

3.5.7 Summary of ecological interpretations with respect to charr biology

It has been necessary to qualify many of the ecological interpretations in this chapter due to uncertainties associated with the parasite life cycles but two features are not in doubt. First, the very existence of parasites utilising planktonic intermediate hosts implies that zooplankton is an important part of the charr diet. Second, the high degree of dispersion implies considerable heterogeneity in feeding habits within each size class. Neither of these inferences could be deduced from Chapter 2.

There is also evidence that there is, on average, a diet shift associated with the peak of the larger size mode. The high variance in the parasite distribution, however, implies that this is not a general shift but that the higher average is due to a few individuals being subject to very high infection rates. Cannibalism by a subgroup of Normals is one interpretation of this evidence and it was observed directly on four occasions, twice each in Lakes C and H. That the onset of a greater rate of infection is associated with a size

threshold may also be connected with the hypothesis that charr must reach a certain size before they become effective piscivores (Damsgård 1993).

There is suggestive evidence only for parasite-induced host mortality in Lake H, and merely that it is "not impossible" in Lake C. This does not contradict previous work which also highlights the technical difficulties inherent in establishing clear evidence of parasite-induced host mortality from ecological studies of hosts and parasites in their natural habitats (Anderson & Gordon 1982).

Despite parasite-induced host mortality being speculative and cannibalism being infrequently observed, it is worthwhile to consider the population implications of a possible connection between the two. If it is supposed that cannibalism leads to a greater number of parasites harboured by the host and that they are subsequently more likely to die, then there is a natural control on the number of predators in the system. As concluded by May & Anderson (1979), "parasites are probably at least as important as the more usually-studied predators ... in regulating natural populations."

4. General Discussion of Fieldwork and Introduction to Models

4.1 Overview

The previous two chapters presented some basic observations about the population structure, reproduction and feeding ecology of the Arctic charr populations of the Borup Fjord region. A few of these facts are selected in this chapter for broader or more speculative discussion than before. For some of these points, mathematical models will be used in Chapters 5 and 6 as extended thought-experiments.

The models do not claim to be an exact representation of "real life", which in any case is not accurately understood due to lack of data, the effects of sampling bias and other unmeasurables. Models are used because they might generate predictions or hypotheses for further experiment or fieldwork. Furthermore, the models might contribute to a synthesis of ideas, highlighting general phenomena and connecting apparently disparate observations with a common process.

4.2 Energy Limitation - A Unifying Concept

Adaptation to energy limitation is seen as the key unifying framework for interpretation of the data. The concept that energy limitation results in trade-offs between the basic life history enhancing features of growth, survival (maintenance) and reproduction is hardly new and Sibly & Calow (1986) argue that knowledge of phenotypic physiology has much to offer in understanding the evolution of adaptations. In particular, they are concerned with physiological adaptations of resource acquisition and use because, they argue, this is not only the basis of the way that organisms function physiologically but also the basis of their form (allocation of resources between different structures) and behaviour (allocation of resources between different activities). They further argue that any one physiological process has to operate within the context of others because the resources available must be shared. This leads to a requirement for the organism to optimise the use of its limited resources between conflicting demands, and trade-offs between physiological processes must occur.

Beyond ecosystem simplicity and an absence of previous human disturbance, perhaps the most significant advantage of conducting research at the latitude of Borup Fjord is that the energetic constraints are amongst the most severe on earth. This leads to the possibility that trade-offs due to energetic constraints will be more obvious than anywhere else. This is confirmed in Section 2.5.4 where the energetic investment in reproduction is shown to be extremely low, so low that Lake H Normal females probably only spawn once per lifetime if they survive.

4.2.1 Size-structured populations

The Borup Fjord lakes contain some classic examples of size-structured fish populations (Chapter 2) and energy limitation is central to the theory on the subject (for review see Werner & Gilliam 1984). This theory supposes ontogenetic niche shifts where a fish can inhabit distinct habitats with different size-specific growth and mortality rates in each. Individuals behaving optimally make the transition from one habitat to another on achieving a critical size at which the ratio of growth to mortality rates has an equal value in the two habitats. The energetic/mortality basis of this is well documented in one recent study, Forseth *et al.* (1994), which demonstrates a shift from benthic to pelagic feeding associated with a reduced cost of feeding for larger charr in the pelagic habitat.

4.2.2 Alternative life history strategies

Alternative life history strategies (e.g. Gross 1984) can also be viewed as representing different ways in which an organism can use the energy available over its lifetime to achieve the same end result of successful reproduction. Within the context of a size-structured population, this could be achieved either side of the critical size where an ontogenetic niche shift might occur. In a two-habitat system, Dwarfs are associated with reproduction below the threshold whilst Normals are associated with reproduction above the threshold. Some systems exhibit more than two habitats, with pelagic charr (Riget *et al.* 1986) or anadromous charr being examples of other valid life history strategies. One system, Thingvallavatn in Iceland, has no less than four landlocked forms (Sandlund *et*

al. 1989). If, as is likely (Chapter 2), energy constraints prevent equally successful reproduction by any one individual in more than one of these habitats then alternative life history strategies arise.

4.2.3 Heterochrony

Flexibility in reproductive status implies operation of the process recognised as *heterochrony* (de Beer 1958, Gould 1977), a process usually applied to phyletic changes in ontogeny, in which the timing of onset, or rate of development of a feature is accelerated or retarded relative to the appearance of that feature in an ancestor's ontogeny.

In the Borup Fjord lakes, it is suggested that heterochrony at the ecological level is manifest by the manner in which the factors governing the combined expression of age and size at sexual maturity are optimised with respect to the genetic demands on somatic growth and the availability of the food supply. Size and age over the reproductive period are thus adjusted to meet the specifics of energy flow within each lake.

Given that the relatively recent ancestors of the present populations were anadromous (Section 1.5), it is probably no accident that each of the size classes exhibits the characteristics of different stages of the Salmonid life cycle such as parr, smolt or adult. So many features of the ancestral life history remain that Klemetsen *et al.* (1989)

propose a relict anadromous life-cycle as a model for landlocked charr in Norway and a simplified version is presented at Figure 4.1. The actual habitats associated with the different sizes of fish are different from those observed in the Borup lakes, but this only serves to highlight the potential flexibility of heterochrony.

Chapter 5 is a model of how an individual would be able to optimise its fitness simply if it were capable of altering the timing of reproduction in response to local conditions. No other physiological process is required, and as such it is a model of heterochrony.

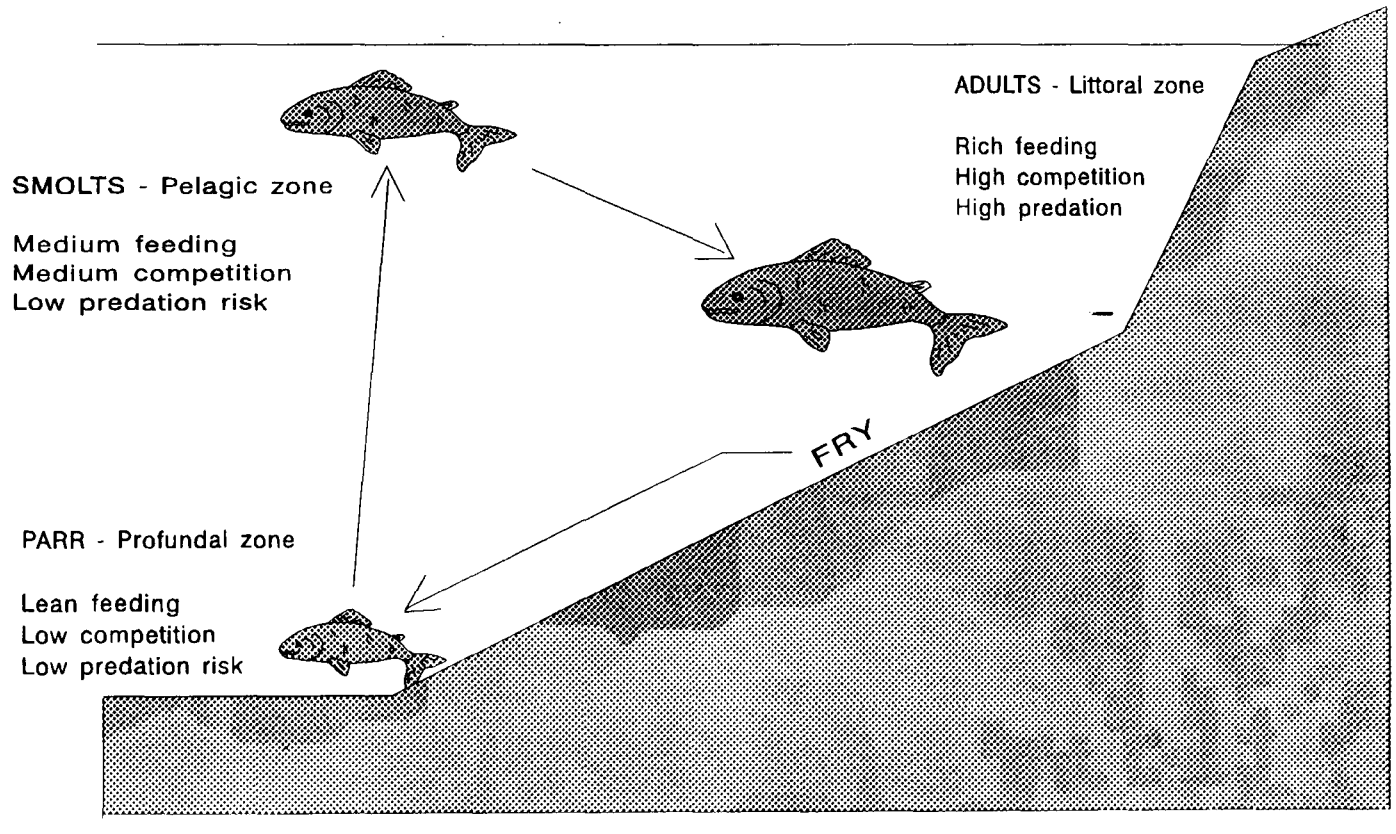


Figure 4.1 Schematic model of the life cycle related habitat shifts by Arctic charr in Takvatn under high population density (adapted from Klemetsen et al. 1989)

4.3 The Missing Mode - A Possible Pelagic Charr

In the largest lake, Lake H, a number of fish of intermediate size and coloration were caught whilst "jigging" and "long-lining" through holes in the ice in May 1988. At the time these fish were regarded as a statistical anomaly and were not seen again in the gillnet sampling conducted in July and August 1988.

Once age data became available, however, age-frequency graphs indicated a lack of samples in the 8 to 15 yr. age range; and especially at 8 to 10 yrs.. The weight vs. age information was even more revealing (Figure 2.7) with a discontinuity occurring at 8 to 10 yrs.. This discontinuity was such that the largest individual charr in the age class increased from 75 g to 570 g between the 9 and 10 yr. age classes. Energetic constraints would almost certainly preclude this massive increase in size in a single year, and imply that more gradual growth is probably occurring via an undetected size mode. Lake C, however, had no such discontinuity. Whilst it can not be proved in the present study, this apparent gap in the data is probably not a result of a poor spawning year at some stage in the past. Johnson (pers. comm.) reports similar observations over successive years with the missing age classes being at the same age on each occasion. This indicates that the "Missing Mode" is a genuine and repeatable feature.

Some clues as to the reason for this discontinuity were given by the observations of Riget *et al* (1986) who found two modes of charr within Lake Tasersuaq, Greenland in July-

August 1982, but a third mode of intermediate size in July-September 1983. This intermediate mode was composed of pelagically feeding fish which became catchable only later in the year when they came inshore to spawn. Sparholt (1985) reports similar difficulties with the capture of pelagic fish.

A number of other indirect clues also pointed to the probable existence of a pelagically feeding size mode in Lake H which was underrepresented in the sampling. These are:-

1. The Normal charr in Lake H had a significantly greater number of gill rakers than Dwarf charr (Section 2.4.10). A high number of gill rakers is usually considered an adaptation for plankton-feeding.

2. Normal charr in Lake H had a predominantly red flesh colour whereas the Dwarfs did not. Henricsson (1977) reports that this is associated with a significant proportion of Crustacea in the diet. The plankton is the only significant source of Crustacea within the Lake.

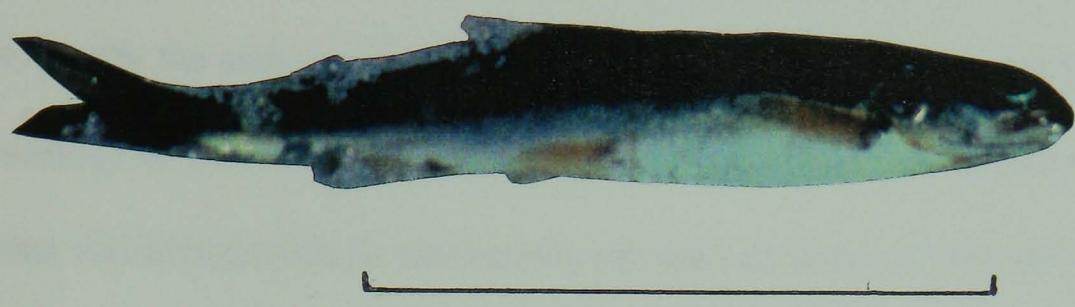
3. An inter-lake analysis of parasite data indicated enormous differences (Table 3.4). This is significant because all the parasites observed in any numbers are known to have copepods as intermediate hosts. The complexities of the parasite life cycles,

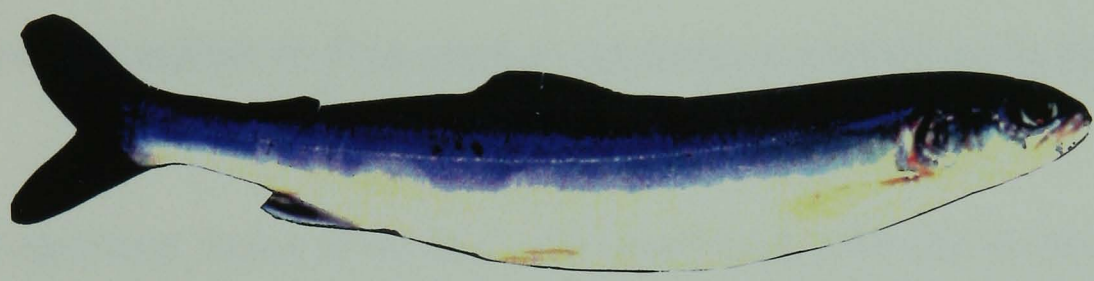
however, mean that it is not possible to make quantitative use of this data as previously discussed in Chapter 3.

As a result of these deliberations, the 1991 fieldwork programme was specifically targeted at resolving the issue of the 'missing mode', and pelagic fish were fished for directly using a 'deep' gillnet, 6 m in depth.

Unfortunately, and despite considerable fishing effort, attempts to catch fish in the pelagic zone met with little success. Two fish were caught on the first occasion the gillnet was used in Lake H on 24th July, but no subsequent samples were obtained. Both fish were exactly as predicted, being of intermediate size and feeding planktivorously upon *Limnocalanus macrurus* Marsh. One of the fish concerned is illustrated in Figure 4.2 along with examples of the other size modes.

The lack of a statistically useful number of samples was disappointing but nevertheless confirms the expectation that any pelagic fish will be at low density. A further factor is that the majority of meshes used in the 'deep' gillnet were unsuitably large for catching fish of this size and schooling may have had some effect. As a result, the area of water actually fished relative to the habitat space was reduced still further. In the unlikely event of another opportunity to return, it would be wise to sacrifice the pretence of obtaining a representative sample achieved by using different mesh sizes and use as large an area of suitable mesh as can be handled.





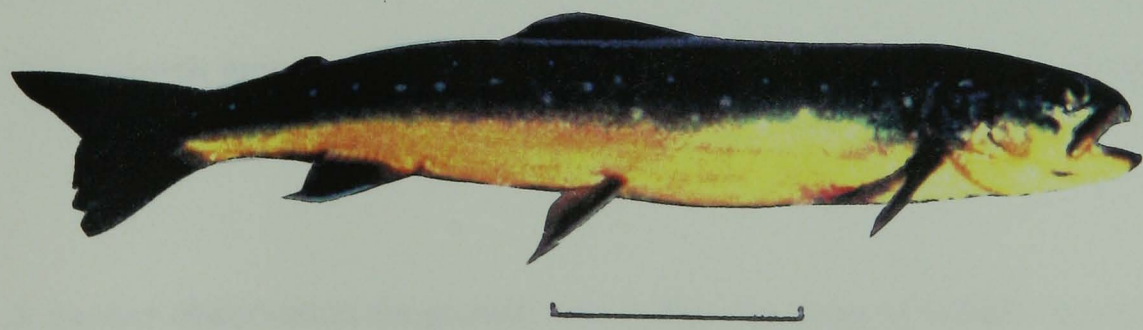


Figure 4.2 Colour photographs (from top) of Dwarfs, Normals and the 'missing mode' from Lake H.

The photographs are not to scale. The bar alongside each fish is approximately 10cm.

Despite the lack of direct evidence it is maintained that the indirect evidence is sufficient to justify the assertion that feeding on zooplankton is an important part of the population ecology of Lake H. The data in Chapter 3 also supports this assertion. It is speculated that this is important in maintaining the high numbers of Normals relative to Dwarfs in this system by providing an "energetic pathway" between the two modes. The significance of this pathway is further expanded upon after consideration of the model of Chapter 6.

4.4 Variation in Population Structure and Growth Rates

A significant feature of the data is the considerable difference in the relative numbers of Dwarfs and Normals between lakes. This correlates with differences in individual growth rates, with low average growth rates being associated with high numbers of Dwarfs. There is, however, far too little data to make firm conclusions on this point but other workers have noted a similar result with anadromous fish. Hindar *et al.* (1991), for example, showed that resident (i.e. non-migratory) behaviour was associated with slow growth amongst the parr of Norwegian Brown trout, *Salmo trutta*.

A further observation on growth rate is that the plots of weight against age indicate a considerable variation in growth rate within each lake as well as between them. The growth trajectories (Figure 2.7) suggest that the Normal fish are derived from the faster growing segment of the Dwarf population, although Lake H data are somewhat confused

by the probable existence of the "missing morph" which was not successfully sampled (this Chapter). A similar situation has been noted in Thingvallavatn where Snorasson *et al.* (1989) concluded that planktonic-char and piscivorous-char from Thingvallavatn, Iceland "may be ontogenetic morphs from the same population" and that "back-calculated growth curves show that piscivorous-char were derived from juveniles that were slightly, but significantly, larger on average than planktonic-char of the same age".

These observations, neither of which can be regarded as providing definitive proof, lead to the following questions:-

Q1. What is the relation between growth rate as a juvenile and life history strategy?

Q2. Which is the fitter animal - Dwarf or Normal?

Q3. Do good growth conditions during the juvenile stages imply that a greater proportion of Normal charr will exist within the population at equilibrium?

Question 1 is tackled by the model of Chapter 5, whilst questions 2 and 3 form the first part of Chapter 6.

4.5 Potential Speciation

Segregation into two sympatric forms exhibiting morphological and ecological differences is not unique to Arctic charr, as McPhail (1984) and J. D. McPhail, University of British Columbia (pers. comm.) point out, sibling fish species are particularly common in formerly glaciated areas and are therefore of relatively recent origin (Svardson 1961, Lindsey 1963, McCart 1970, Henricson & Nyman 1976, Copeman 1977, Bodaly 1979). McPhail has described comparable situations in sticklebacks, *Gasterosteus aculeatus* L., in the fresh waters draining into the Strait of Georgia, British Columbia, in which morphological and ecological differences are correlated. However, McPhail has established in the case of *Gasterosteus*, that the differences between the two forms in certain lakes are inherited and are "not part of a complex trophic polymorphism". On the other hand, Hindar *et al.* (1986) reject the multiple species hypothesis. They found that genetic distances between populations of Arctic charr from 15 different localities in Norway were extremely small when 42 electrophoretically detectable loci were examined. Five of these localities contained both Dwarf and Normal charr.

Morphological difference (gill rakers) was detected in Lake H (Chapter 2), but the lack of molecular evidence means that it is impossible to state where on the possible spectrum of genetic relationships the Borup charr morphs lie (Samples were taken on behalf of other workers for this purpose, but the high cost of work in this area has meant that no results are yet forthcoming). An alternative approach tackles the question through the

model of Chapter 6. The question is synonymous with the "charr problem" and is summarised as:-

Q4. Are the different size modes of charr within each lake genetically divergent? If so, what is its ecological significance and how is the divergence maintained?

5. A Model to Illustrate the Ecological Significance of Growth Rate Variation

Growth or Reproduction? - A life history gamble

Supervised by Professor Roger Nisbet

5.1 Chapter Abstract

A qualitative mathematical model is used to demonstrate how overall lifetime fitness can be optimised by changing the timing of reproduction with respect to somatic growth. In the case of a bimodal population where mature individuals exist within both size modes, two potentially successful strategies arise. These strategies are labelled the Dwarf and Normal strategies, and the Dwarf strategy is optimised by allocating resources to reproduction whilst a member of the smaller mode. By contrast, the Normal strategy is optimised by allocating resources to growth whilst a member of the smaller mode and, following recruitment to the larger size mode, subsequently to reproduce. The strategies are predicted to be optimised at different growth rates.

5.2 Introduction

This chapter is based on a paper presented at the American Fisheries Society conference on Fish Ecology in Arctic North America in May 1992. The paper has been accepted for inclusion within the proceedings but is yet to be published. Since the time of the conference, a degree of work has been conducted independently by other workers which extends the concepts from the deliberately simplistic level presented in this chapter. A section on this more recent work is included within the latter part of the discussion.

The model examines the implications of alternative life history strategies and heterochrony within the energy constraints of a size-structured population. As such, it is a mathematical restatement of section 4.2 in the previous Chapter. The simplest case of a size-structured population, the bimodal situation, is used and the model analyses the alternative life history options available to members of the smaller mode.

The evidence of Chapter 2 suggests that different, semi-discrete habitats support an optimal size of fish characterised by the modal value of the appropriate morph. Other work also recognises the association between the size of a fish and its habitat. Examples include the profundal, pelagic and littoral habitats defined for Arctic charr from Takvatn by Klemetsen *et al.* (1989); or the piscivorous, benthic and planktonic habitats defined for Thingvallavatn fish by Sandlund *et al.* (1989).

In the model, "habitat" is defined somewhat more abstractly in terms of the energetic constraints it places on the individual and, within these constraints, the trade-offs which might occur between growth, reproduction and survival. The fittest strategy is the one which most successfully optimises these trade-offs. In the two-habitat bimodal population, each habitat is described by a different set of constraints and trade-offs. For Dwarf and Normal sub-populations which simultaneously occupy two separate habitats, an individual must obtain a threshold size, W_{th}, (Figure 5.1) in order to exploit the richer, Normal habitat. The Normal habitat is not available to the Dwarf individual because it is excluded by a dominance hierarchy or fear of predation (Werner *et al.* 1983).

The results of the model are discussed with respect to Chapter 4 Question 1, which asks whether there is a relation between growth rate and life history strategy.

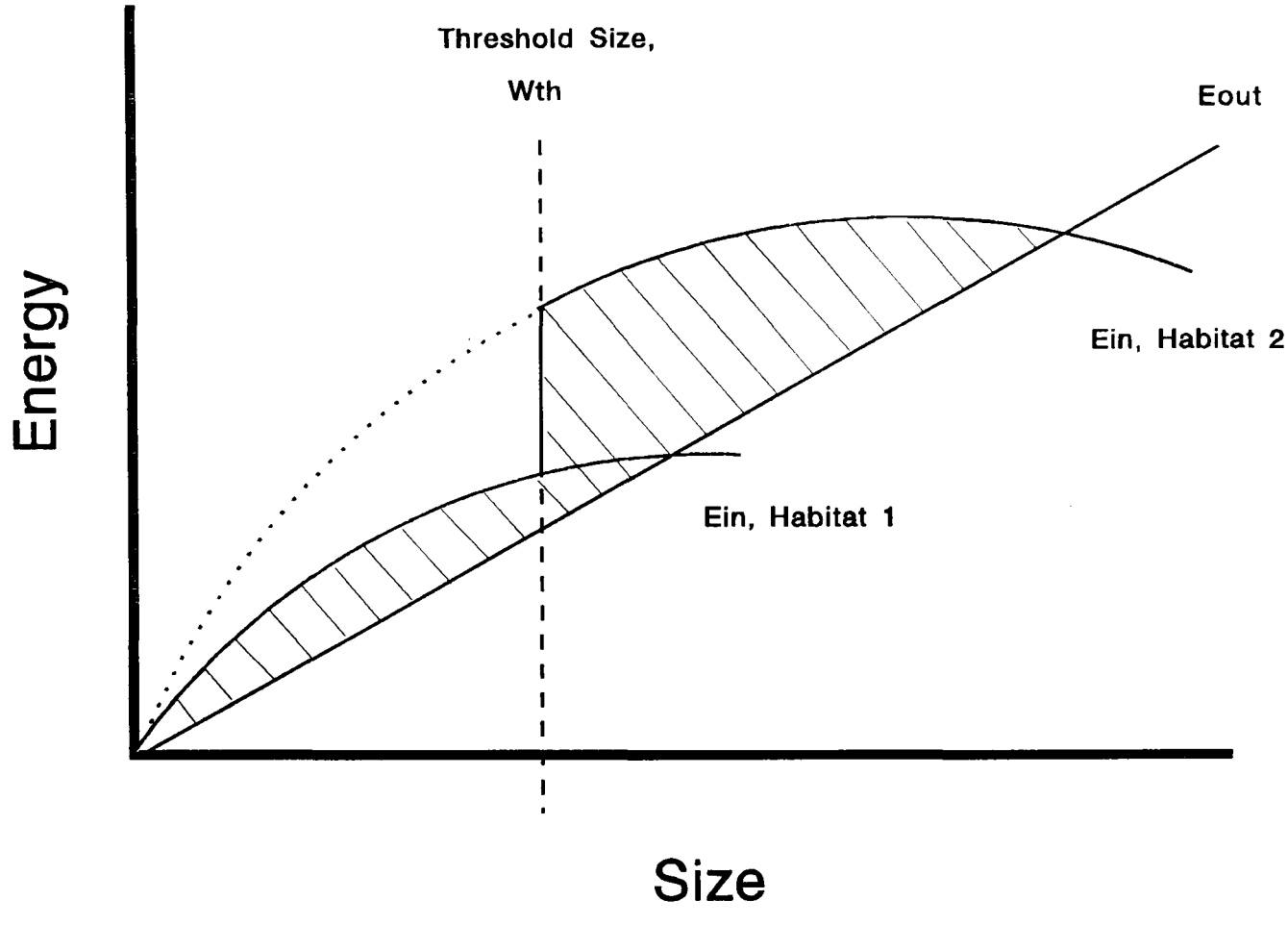


Figure 5.1 Energy available, Ein, and energy costs, Eout, against size for Dwarf and Normal habitats. The richer feeding of the Normal habitat is only available once an individual reaches Threshold Size W_{th}..

5.3 A Simple Model of Energy Limitation and Trade-offs

5.3.1 Energy constraints

The fundamental energy constraint is modelled by von Bertalanffy growth which supposes that access to greater resources is traded against higher maintenance costs. Von Bertalanffy (1960) argued that net energy available for growth (E_{in}-E_{out}) is a balance between resources obtained, E_{in}, and resources used to meet the "cost of living", E_{out}. Catabolism, the breakdown of tissues, proceeds at a rate proportional to body weight, W;

anabolism, synthesis of body tissues, proceeds at a rate proportional to body surface area. Assuming that all available energy is then applied to somatic growth, this leads to the equation:

$$\frac{dW}{dt} = k_2 W^b - k_1 W^a \quad ; \text{where } b = 2/3,\ a = 1; \qquad \text{Eqn.1}$$

t = time; k_1, k_2 = constants

When integrated the familiar sigmoid growth curve results. A more detailed species-specific model might use other values for a and b estimated from experimental growth data (Reiss 1989), or take measured data from energy budget experiments.

5.3.2 Trade-offs

Within the constraints of the von Bertalanffy equation, it is supposed that the fish is able to allocate energy in any way to growth, reproduction and survival; but only within its energy budget. Energy "spent" on one of the life history enhancing factors of is not available for the others, and trade-offs result as follows:-

Growth vs. Reproduction: The mass of eggs spawned is related to body size at spawning. For females the mass of eggs spawned is approximately proportional to (Weight, W)$^{1.2}$ (Chapter 2).

Mortality vs. Reproduction: It is supposed that charr spawn only once. This is a fundamental constraint on an individual's life history as once an individual has spawned it ceases to contribute to the population in fitness terms because it has no further offspring. This assumption is justified in females (other than from Lake A) by the data in Chapter 2, but it represents an extreme situation. In most systems, iteroparity is usual and hence this constraint is less severe.

Growth rate vs. Mortality: The shape of the weight against age plots at Figure 2.7, especially those for Lakes C and H, indicate that the fastest growing fish reach the largest individual sizes in the population but are not the longest living. Fish exhibiting a more moderate growth rate, however, are the oldest but not the largest fish in the population. This implies an inverse relationship between growth rate and survival rate. Whilst these plots are by no means unusual and are typical of many fish populations, these particular plots are of completely unexploited populations and this reduces the number of other interpretations which could be placed on this observation. In the absence of quantitative data, however, the model uses an educated guess followed by an analysis of the robustness of the general result to variations in the expressions used. The example chosen is an adaptation from Sibly & Calow (1986), where:

$$Z = 0.1 + \frac{u^2}{5} \quad , \quad Z = \text{instantaneous mortality rate}$$

$$u = \frac{1}{W} \cdot \frac{dW}{dt} \qquad \text{Eqn. 2}$$

The relationship between growth rate and mortality is modelled by the term, u, with the 1/W term indicating reduced mortality at larger size. Survival to time t, is calculated as:

$$S(t) = \exp\left[-\int_0^t Z(t).dt\right]$$

5.3.3 Heterochrony and definition of fitness

In this model, fitness is defined as the size of an individual's gonad at spawning multiplied by the probability of it surviving to spawn. Heterochrony is modelled by supposing that the individual can spawn at any time, with fitness calculated for all possible ages at spawning. The optimal age at spawning is associated with a maximum in the fitness function. Seasonality is ignored which means that any distinction between interannual and seasonal differences in timing is lost.

5.3.4 Alternative life history strategies

Two strategies are available to members of the smaller size mode (Figure 5.2.). Different members of the population may simultaneously adopt either strategy but it is supposed that energetic constraints prevent an individual from successfully adopting both:-

Dwarf Strategy: The individual adopting the Dwarf strategy spawns as a Dwarf.

Normal Strategy: The individual adopting the Normal strategy spawns as a Normal. In this case, the first part of its life history strategy is to reach the threshold size, W_{th}, of the Normal habitat with minimum mortality. The second phase is to optimise the timing of reproduction within the Normal habitat. The model effectively makes the assumption that these two phases are independent of each other and thus that, for example, optimisation of the recruitment phase does not commit the animal to a sub-optimal reproduction phase. This assumption is thought to be reasonable since selection will presumably have occurred in favour of achieving a "double optimisation".

5.3.5 Optimisation

It is assumed that the von Bertalanffy parameter, $k_1 = 1$, which defines the "cost of living" is constant for the hypothetical phenotype examined. The parameter, k_2, is allowed to vary, but only subject to the trade-offs defined above. Optimisation of the Dwarf strategy" effectively occurs in three dimensions. For every value of k_2, there is an optimal age at reproduction; but there is only one value of k_2 associated with the highest possible fitness.

Optimisation of the Normal strategy is only calculated for the first phase of its life history strategy; that of achieving threshold size, W_{th} , with minimum mortality. Optimisation finds the value of k_2 which achieves this with minimum mortality. Appendices A and B are the PASCAL programs which calculate the optimal value of k_2 for the Dwarf and Normal strategies respectively.

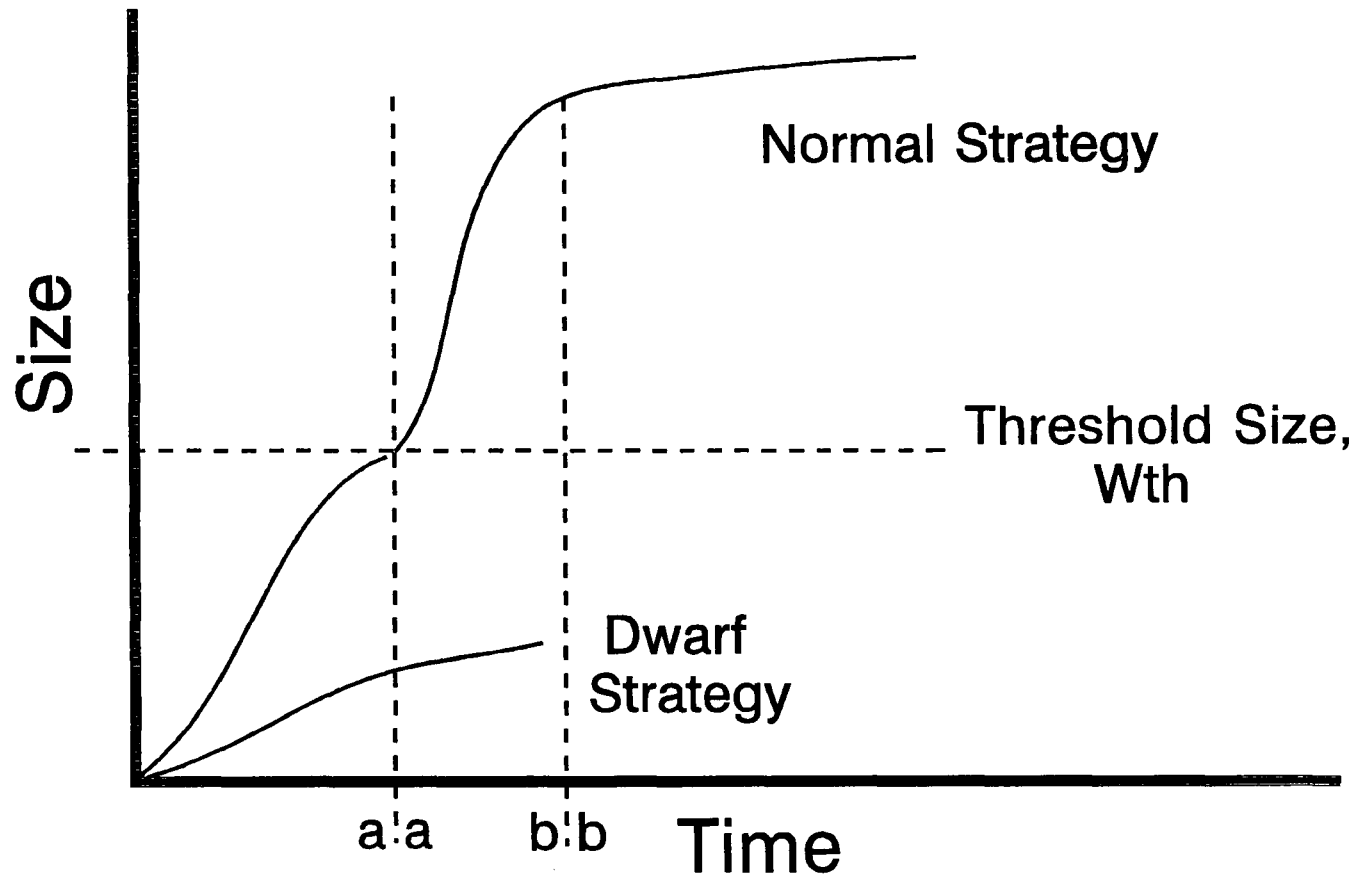


Figure 5.2 Two alternative life-history strategies available to an individual in a bimodal population. The Dwarf strategy is associated with an optimisation in the timing of reproduction and growth within the Dwarf's habitat. The Normal strategy is associated with achieving recruitment to the Normal habitat with minimum mortality and, subsequently, reproducing within the Normal's habitat. The growth interval aa-bb corresponds to a period of saltatory ontogeny (Balon 1984 b) as the individual shifts from one habitat to the next.

5.4 Results

Dwarf strategy: Assuming that reproduction is possible at any age, the combined effect of increasing size and decreasing survival leads to a local fitness maximum for any value of k_2 (Figure 5.3). In addition, there is an optimum k_2 which pertains to the maximum possible fitness which can be obtained if any value of k_2 is physiologically possible. In this case, the optimal value of k_2 is 3.28 (Figure 5.4).

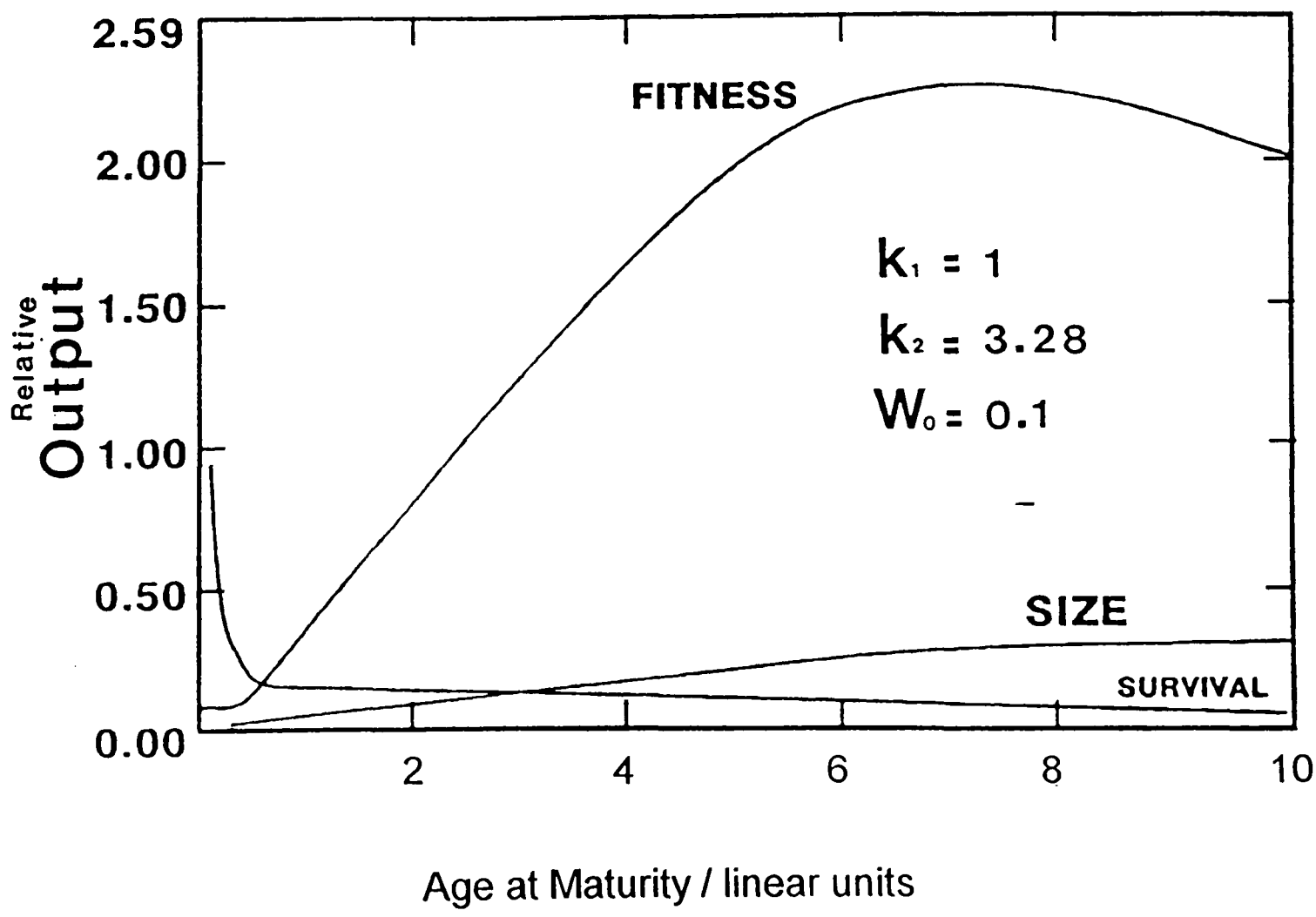


Figure 5.3 Typical behaviour of survival, fitness and size with age at maturity for the Dwarf strategist spawning within the smaller size mode. The model calculates the fitness achieved for all possible ages at maturity. The optimal age at maturity is associated with the maximum calculated fitness value.

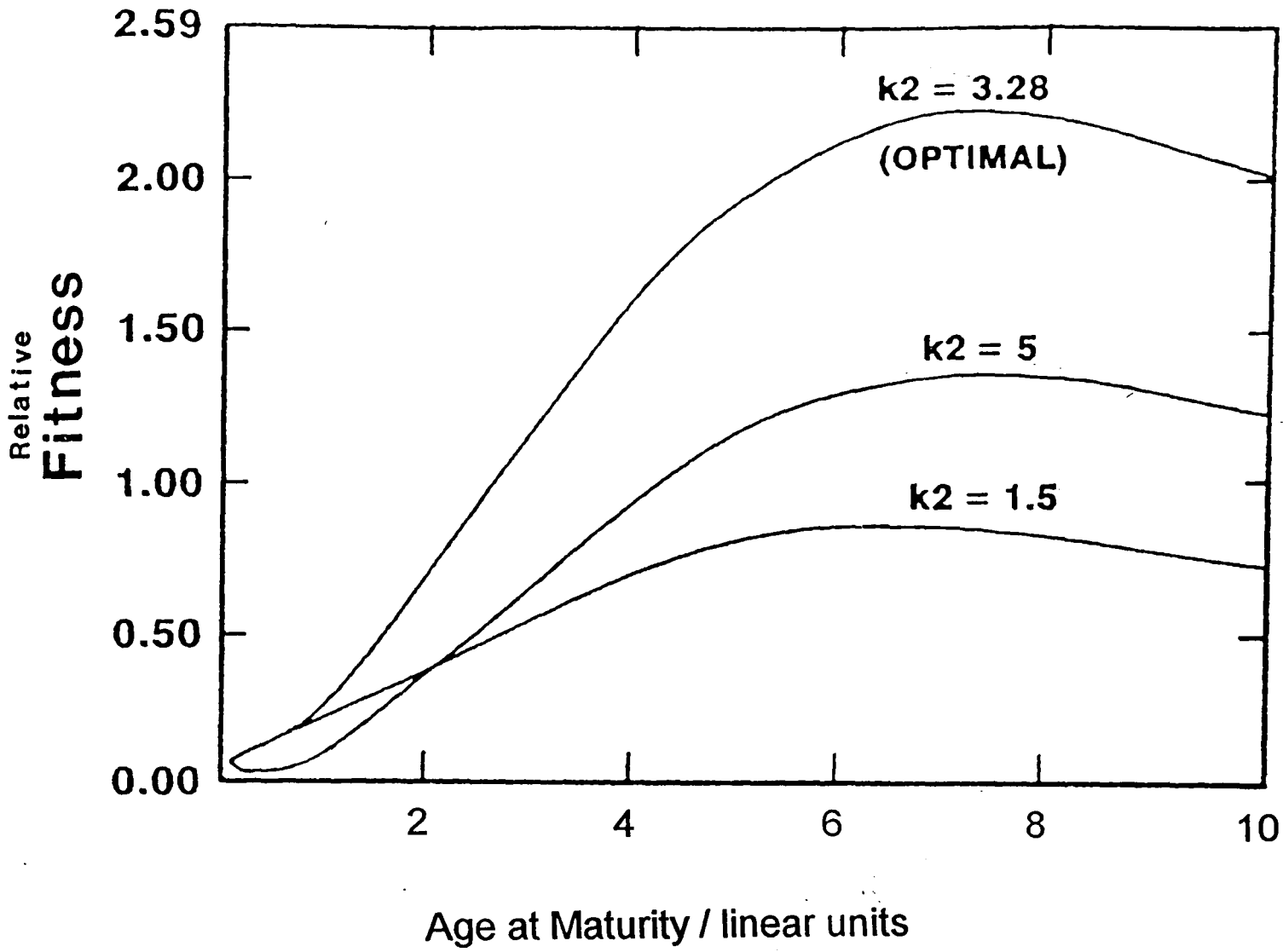


Figure 5.4 Comparison of relative fitness for the Dwarf strategist given different levels of commitment to growth.

Normal strategy: The optimum value of k_2 for the Normal strategy depends on the value of the threshold recruitment size, W_{th}, under consideration. Consider size-survival curves for two different values of k_2 (Figure 5.5). The crossover corresponds to where one k_2 becomes less risky than the other, and shows that a low k_2 will prevent a slow-growing fish from ever reaching threshold size. The values of optimal growth rate parameter, k_2^*, required to achieve various threshold sizes, W_{th}, with minimum mortality, S_{max}^*, are at Table 5.1. Any threshold size greater than the optimal size at maturity required by the Dwarf strategy requires a higher k_2^*, and hence higher growth rate.

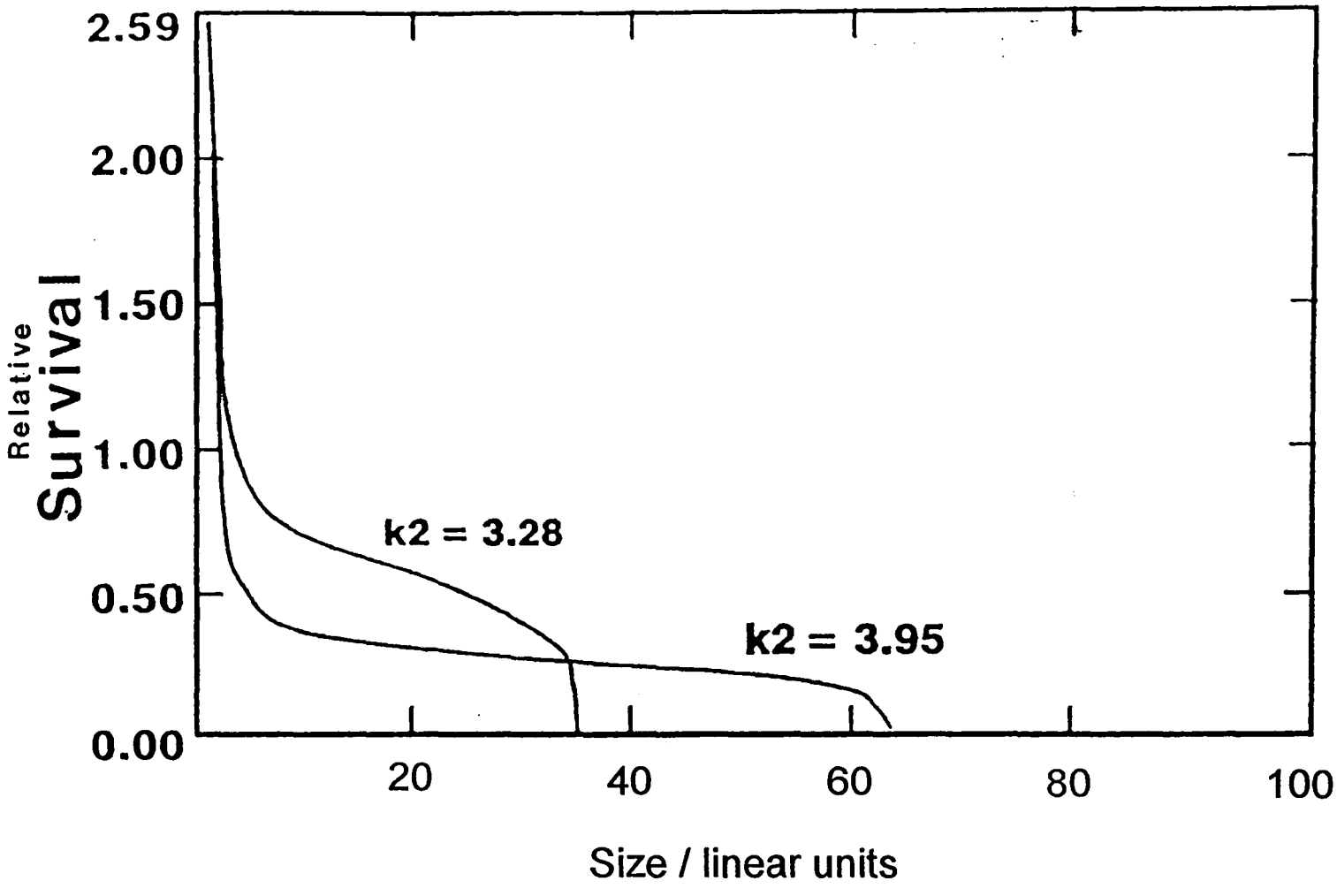


Figure 5.5 Relative chances of survival to given size assuming two different levels of commitment to growth.

k_1	W_{th}	k_2^*	S_{max}^*
1	75	4.45	0.0103
1	50	3.95	0.0195
1	27.9	3.28	0.0425

Table 5.1 Optimal growth and survival parameters for an individual growing to a given size, W_{th}. k_1, k_2^* are the optimised von Bertalanffy parameters and S_{max}^* is the value of the proportion of individuals surviving from birth to recruitment to the Normal sub-population at size, W_{th}.

Predictions: It is predicted from the above that fitness is maximised for the Normal strategy at a higher growth rate than for the Dwarf strategy during the phase when the individual occupies the smaller size mode. This is consistent with the tentative observations of Section 4.4. The model is, however, sensitive to the exact nature of the growth-survival trade-offs which are not well-known, and also the definition of fitness. Given that seasonality is also ignored, this result is, therefore, not robust and probably not general. The prediction that the Dwarf and Normal strategies would normally be optimised at different growth rates more closely reflects these considerations of the validity of the assumptions.

5.5 Discussion

5.5.1 Model sensitivity

A major difficulty in most studies of life history strategies is the lack of accurate information relating to mortality and, other than an ability to discern basic trends, the Borup data are unfortunately no different. Over and above the normal problems of sampling bias within any given habitat (Chapter 2), determining mortality rates is almost intractably complicated for multimodal populations. Assuming that the model of ontogenetic succession (Figure 4.1) is accepted, there are two predominant reasons for this:

(1) Individuals within different habitats behave differently and thus have different susceptibilities to fishing methods (Section 2.5.1). Inter-habitat sampling bias is thus inevitable.

(2) When an age class recruits from one habitat to the next and, given (1) above, it is impossible to determine what proportion of the age class has recruited to the next habitat and what proportion has suffered genuine mortality.

These uncertainties in the mortality data are the main reason why the model does not allow quantitative predictions to be made.

The qualitative nature of the model and also its sensitivity is mirrored in nature by examples of sexual dimorphism and sex ratio differences frequently observed in Arctic charr and other salmonids (Johnson 1980, Jonsson & Hindar 1982, Chapter 2). In the Borup Fjord study (Chapter 2), males spawned more frequently than females and the gonadosomatic index decreased with size for males, but increased for females. However, the modal size of Dwarf males was less than females with the situation reversed for Normal charr. It is probable that these observations are related and that the slightly different reproductive strategies adopted by opposite sexes sharing the same environment might be leading to different optimal solutions to life history trade-offs. Further examples are given in Section 5.5.3.

5.5.2 Heterochrony

Potential confusion exists with the meaning of "heterochrony" because the term has been applied in many contexts. For the purposes of this thesis it is used on the level of whole organism ontogeny to describe changes in the timing of thresholds in life history (Bruton 1989). These changes allow the organism to match the appropriate life history style with the appropriate environment for the right length of time in order to take advantage of favourable conditions for that particular life interval, or to await favourable conditions in the next life interval. Amongst other examples, Noakes *et al.* (1989) also use the term with this meaning to discuss heterochronic shifts in ontogeny in relation to niche utilisation as a proximate mechanism for the widespread phenomenon of phenotypic variation within salmonid species. Given this definition, the model is effectively about heterochrony since it shows how variation in the timing of reproduction with respect to somatic growth can achieve optimisation of a spectrum of life history strategies without the need for any other physiological change.

Balon (1984 a,b) argued that the Dwarf/Normal situation is an example whereby epigenesis (the interaction among gene products, cells, tissue, organs and the environment in the formation of the organism) has caused the formation of an "altricial <=> precocial dynamic state". Balon proposes that the mechanism for the formation of these altricial <=> precocial pairs is saltatory ontogeny. Saltatory ontogeny requires that structures align their rates of development to become complete simultaneously and that a new function is initiated by a rapid transition from one stabilised state to another. Significantly, Balon also cites heterochronic processes as a

mechanism. In this paper the model links Balon's concept to different life history options for utilisation of scarce resources, and saltatory ontogeny is demonstrated by the period of rapid growth which results whilst the Dwarf charr is recruiting to the Normal sub-population. (This period of fast growth is shown as the interval aa-bb in Figure 5.2).

The ecological significance of heterochrony as manifested in multimodal Arctic charr populations via saltatory ontogeny and altricial <=> precocial dynamic states is considerable. It provides a mechanism for a single phenotype to adapt to the changing specifics of energy flow within a rapidly changing environment. Variation in age and size at maturity, and growth rates, between otherwise similar fish is likely to be a result of this process. On a note of caution, however, the illustration of heterochrony provided by this model alone does not *prove* that it is wholly or even partially responsible. It merely shows that a large range of observations *could* be explained and connected by this one mechanism.

5.5.3 Recent work on alternative life history strategies in Salmonids

This chapter is rework of the paper presented at the American Fisheries Society conference on fish ecology in Arctic North America in May 1992. The following is an extension to the discussion which covers work published since that time and evidence from other salmonids.

An important feature of the model is that it predicts that there are circumstances where the faster growing component of a population can reach reproductive maturity later (but at a larger size) than the slower growing component. This is contrary to the almost invariant rule (Alm 1959) that faster-growing fish mature first, but a greater than cursory glance at this seminal paper indicates that Alm was careful to qualify this rule as applying only to the same species or form. This shows that he also understood that the presence of alternative life history strategies might disrupt this finding and there are many examples (some within Alm's paper) of where this qualification is necessary. For example, Svedäng (1991) found in a rearing experiment that there was a significant negative correlation between maturation rate and growth rate in male Arctic charr; a relationship which was also reflected in females but not with statistical significance.

A great degree of further insight into the significance of growth rate variation can also be gained by extending the literature search to other Salmonids, particularly Atlantic salmon, *Salmo salar*. Generally, the admissibility of the information obtained requires acceptance that there is an analogy between the Dwarf/Normal situation in landlocked charr and precocious maturity/smolting in migratory salmonids. In rearing experiments, Thorpe *et al.* (1989) showed that the percentage of smolts at age 1 was correlated with an "index of growth opportunity" during the July post hatching. A geographical analysis (Metcalfe & Thorpe, 1990), applied using an index of annual growth opportunity, showed that the average age of smolting in 182 Atlantic salmon rivers over a 40° latitude range implied a similar relation to growth rate over a longer timescale. Studies of Atlantic salmon parr (Metcalfe & Thorpe 1992, Huntingford *et al.* 1992) have shown

that early smolting as a life history strategy is associated with early first feeding, dominant status and membership of a faster-growing component of the age class. Metcalfe *et al.* (in press) correlate these characteristics to a high metabolic rate in juveniles. Similar evidence is provided in anadromous Arctic charr (Svenning *et al.* 1992) and Masu salmon, *Oncorhynchus masou* Brevoort (Hirata *et al.* 1988).

Unfortunately, even within Salmonids, it is not possible to generalise about the relation between alternative life history strategies and growth rate since many populations (e.g. Hutchings & Myers 1994) exhibit early maturity by young, fast-growing, males. This is hypothesised to be due to seasonal effects which are ignored by this chapter, but even in this case the two life history strategies are characterised by different growth rates which is the extent of the prediction made by this model.

All the above evidence indicates that the existence of alternative life history strategies is indeed associated with different juvenile growth rates. Whilst it is admitted that seasonality is an issue that should have been better addressed in the original paper, it was always recognised that the inability to define accurately the nature of the trade-offs on the individual life histories meant that actual prediction of the values of observed growth rates was beyond the scope of the model. It is thus argued that the additional evidence presented supports the general conclusions unchanged and also that there is still insufficiently accurate trade-off information available to proceed to a quantitative model.

6. Models of Population Structure and Potential Speciation

Supervised by Professor Roger Nisbet

6.1 Chapter Abstract

Simple mathematical models are used to caricature density-dependent interactions within and between Dwarf and Normal components of a bimodal population. Two different assumptions concerning the genetic relationship between the two alternative life history strategies are investigated: complete reproductive isolation; or a single stock which chooses alternative life history strategy facultatively. In constant environmental conditions, the Evolutionarily Stable Strategy (ESS) (Maynard Smith & Price 1973) is not affected by these assumptions and the ESS proportions of Dwarfs and Normals are shown to vary with environmental parameters. In particular, a high proportion of Normals is thought to be associated with high growth rate as a juvenile; and a "stunted" or unimodal population with low growth rates. A difference in the ratio of fecundity to mortality rate (r/μ) between Dwarf and Normal sub-populations is also shown to be essential to maintaining bimodal populations and it is argued that cannibalism is one mechanism which could achieve this difference. The predicted ESS for selection of the Normal strategy is similar to that observed experimentally in the analogous case of smolting in Atlantic salmon (Thorpe *et al.* 1989). The model is extended to ask what ecological conditions would favour evolution towards the speciated or reproductively-isolated state. It is concluded that short term environmental fluctuations select against speciation and that most natural bimodal Arctic charr stocks will achieve maximum individual fitness within a "semi-speciated" configuration which is maintained by incomplete assortative mating.

6.2 Introduction

Where alternative life history strategies exist, selection is occurring at two levels:- first on the choice[5] of life history strategy itself and thereafter on maximising individual fitness within that strategy. Whilst much theoretical work has been conducted (e.g. Stearns & Koella 1986) on the evolution of life history traits within strategies, and Chapter 5 is a variation on this theme, little has been done on the more fundamental choice as to which life history strategy to adopt in the first instance. This chapter is about that choice and the mechanisms, genetic or otherwise, by which this might be determined.

6.2.1 Population structure

How many individuals choose which strategy has important implications to population structure since, for example, the higher the proportion of fish which choose the Normal strategy (Chapter 5), the more members of the larger size mode there are likely to be. Density-dependent interactions within and between sub-populations of Dwarfs and Normals will, however, affect the relative success of any particular individual dependant upon its choice of life history strategy. This means that there is feedback between population dynamics and optimal choice of life history. These interactions and feedback are modelled in this Chapter, and provide evidence to answer Chapter 4 Question 2 which asks which of Dwarfs and Normals are the fitter.

[5] The term "choice" is not intended to imply a conscious decision, but is used as shorthand for the complex gene versus environment interactions which might determine the life history strategy adopted by an individual.

The equilibrium conditions of the model define the population structure which will arise for any given set of environmental parameters. This is discussed with respect to Chapter 4, Question 3 which asks whether good growth conditions as a juvenile correlates to a greater proportion of Normals in a population. Fisheries management is also discussed because there is a significant commercial premium on maintaining population bimodality. The alternative unimodal, or "stunted", populations consist of small fish of little commercial value (Paper V, Damsgård 1993).

6.2.2 Potential speciation

How the individual determines choice of life history strategy has no implications at all to population structure, but important ones to questions of speciation. At one extreme, Dwarfs and Normals could be separate species with the choice being determined entirely genetically. At the other extreme, the choice could be determined by a reaction norm adopted by a single genotype. The term "weighted coin" is used as shorthand for this reaction norm. Alternative, but more wordy, terminologies for the same process include "adaptive coin-flipping" or, more properly still, "intra-genotype strategy mixing" (Cooper & Kaplan 1982). It is supposed that the form of this "weighted coin" is not at all random and that it has been selected for. The models are used to calculate the optimal "weighted coin" as a function of the environmental parameters. The function obtained is compared with experimental evidence from the analogous situation of smolting in Atlantic salmon (Thorpe *et al.* 1989).

By combining the two extreme assumptions about genetics into one model and paying particular attention to environmental fluctuations, it is asked under what circumstances selective advantage might arise if the competing life history strategies were to evolve towards speciation. This is tackling the first part of Chapter 4 Question 4. The final part of Chapter 4 Question 4 asks how such genetic divergence is maintained, and this is not tackled directly although potential mechanisms are discussed.

6.3 Simple Models of Bimodal Population Structure

The models rest on the assumption that the population is size-structured and that all juvenile fish share a single habitat. Dwarfs reproduce in this same habitat whilst Normals shift to a new habitat at some size threshold and thereafter continue to grow prior to reproduction. Thus a lake containing two habitats, $H1$ and $H2$, is modelled with Dwarfs and juvenile Normals in $H1$ and adult Normals in $H2$. Recruitment to both habitats is limited by the density of individuals *already in the habitat*, an assumption intended to provide a crude representation of factors as diverse as territorial behaviour or cannibalism whereby "residents" repel "immigrants", an assumption previously proposed for Arctic charr in the (verbal) model of Johnson (1976).

As it is wished to investigate the significance of the genetic relation between Dwarfs and Normals, three models are studied:

A. *Separate stocks model.* Dwarfs and Normals are different species.

B. *Single stock model.* Dwarfs and Normals are recruited from a single gene pool, with the "weighted coin" allocating individuals to each life history strategy simultaneously with entry to habitat $H1$.

C. *Speciation model.* There are three "species": pure Dwarfs, pure Normals, and "mixed strategists" (individuals equipped with the "weighted coin" from model B)

Note that in model B, the "decision" to adopt the Dwarf or Normal growth strategy while in habitat 1 is made soon after hatching. The model equations are listed in Tables 6.1, 6.2 and 6.3 and illustrated in Figures 6.1 and 6.2. The models consist of coupled continuous-time differential equations which describe the flow of individuals through each state in the form:-

Rate of Increase = recruits IN - deaths - emigrants OUT

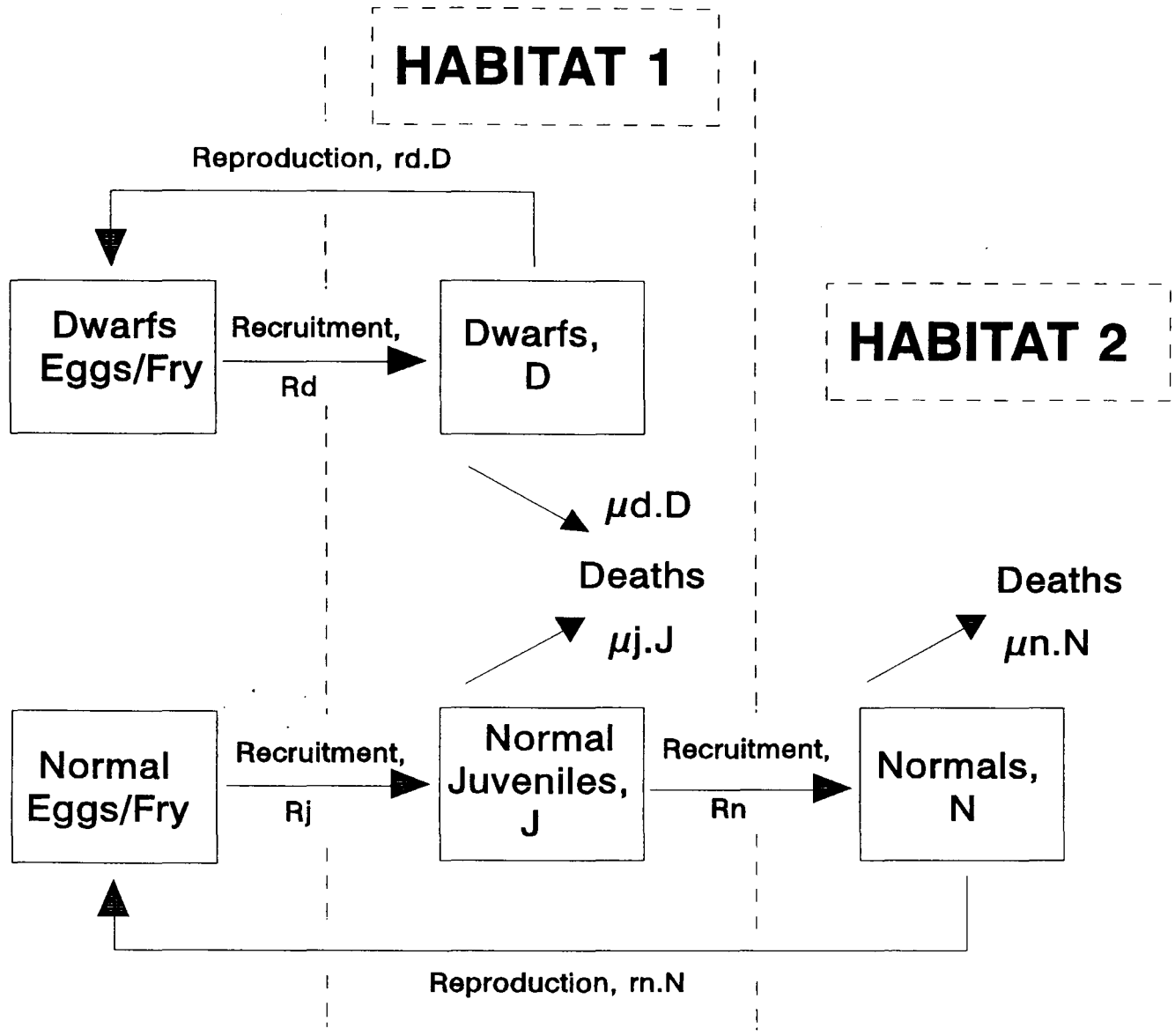


Figure 6.1 Model of two reproductively-isolated stocks of Arctic charr coexisting in a speciated state within the same lake. (Model A). Density-limited recruitment occurs between each habitat and no individual is capable of spawning in more than one habitat.

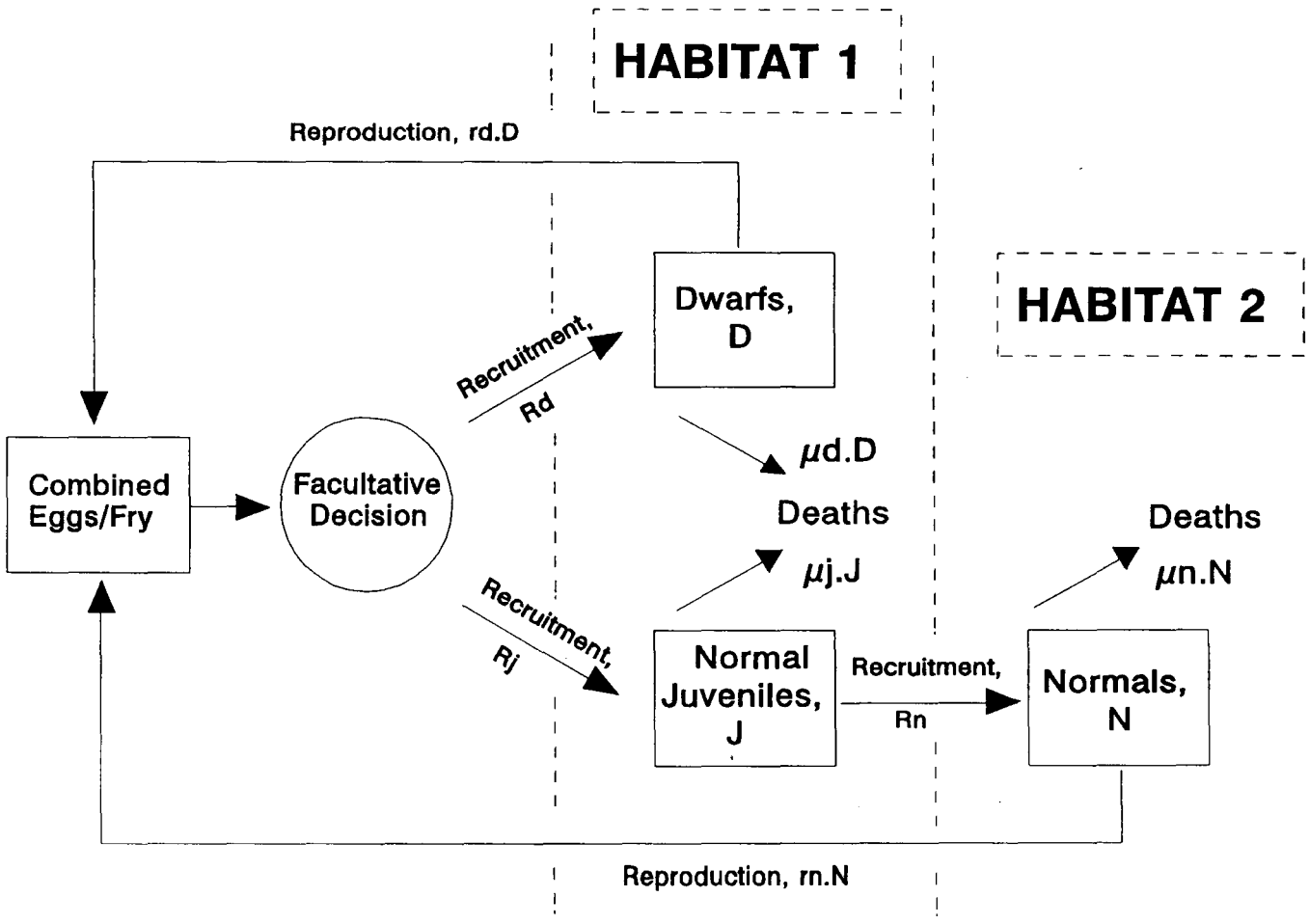


Figure 6.2 Single stock model where individuals are subject to the same constraints as for the separated stocks model but contribute to a single gene pool. (Model B). Choice of Life History strategy is determined by a 'weighted coin'.

	Symbol	Default Value	Units	Brief Description
Variables	D		Individuals	Mature Dwarfs
	J		Individuals	Juvenile Normals in Dwarf Habitat
	N		Individuals	Mature Normals
	t		Time units	Time
	P_d		Dimensionless	Probability of selection of Dwarf life history strategy (Single stock model only)
	P_n		Dimensionless	Probability of selection of Normal life history strategy (Single stock model only)
Parameters	r_d	1.5	Time^{-1}	Individual Dwarf fecundity rates
	r_n	6.0	Time^{-1}	Individual Normal fecundity rates
	μ_d	0.125	Time^{-1}	D mortality rate
	μ_j	0.125	Time^{-1}	J mortality rate
	μ_n	0.125	Time^{-1}	N mortality rate
	K_d	10	Individuals	Dwarf habitat carrying capacity
	K_n	10	Individuals	Normal habitat carrying capacity
	G	1.7	Indivs./time	Recruitment Factor
	D_o	0.01	Individuals	Recruitment restriction term

Table 6.1 Variables and parameters used in the bimodal population models.

	Symbol	Separate Stocks	Single Stock
Recruitment Rates	$R_d =$	$r_d.D.\exp(-(D+J)/K_d)$	$(r_d.D+r_n.N).P_d$ $x \quad \exp(-(D+J)/K_d)$
	$R_j =$	$r_n.N.\exp(-(D+J)/K_d)$	$(r_d.D+r_n.N).P_n$ $x \quad \exp(-(D+J)/K_d)$
	$R_n =$	$G.J/(J+D+D_o).\ \exp(-N/K_n)$	
Balance Equations	$\frac{dD}{dt} =$	$R_d(t) \ - \ \mu_d.D$	
	$\frac{dJ}{dt} =$	$R_j(t) \ - \ \mu_j.J \ - \ R_n(t)$	
	$\frac{dN}{dt} =$	$R_n(t) \ - \ \mu_n.N$	

Table 6.2 Formulation of the continuous time differential equations used in the bimodal population models. The only difference between the separate and single stock models is the source of recruits to the Dwarf and Juvenile sub-populations (R_d and R_j). The recruitment terms are defined in Figures 6.1 and 6.2.

Example Term	Biological Interpretation
$r_d.D$, $r_n.N$	The number of eggs produced by each sub-population. r_d is less than r_n owing to the lower growth rate of Dwarfs.
$\exp(-N/K_n)$	Density-limited recruitment to Habitat 2. As N increases, this term becomes smaller.
G	An optimised parameter which simulates the life history 'cost' of reaching minimum Normal size.
$J/(J+D+D_o)$	A term modelling the competitive pressure of individuals adopting the Dwarf strategy on recruiting juvenile Normals. By competing for resources within Habitat 1, Dwarfs are reducing the Juvenile Normal growth rate.
$\mu_d.D$	Number of Dwarfs dying per unit time.
$\exp(-\mu_{di}.T_{dim})$	The proportion of Immature Dwarfs which survive to mature in the stage-structured model (Appendix F).

Table 6.3 Biological interpretations of example model terms.

6.3.1 Optimisation within life history strategies

The models suppose that both strategies are optimised via the processes discussed in Chapter 5. The optimised Dwarf Strategy is characterised by an age and size at maturity within Habitat 1. The optimised Normal strategy is characterised by a minimised probability of mortality prior to recruitment to Habitat 2, followed by a larger age and size at maturity within Habitat 2. The three stages of optimisation are characterised by parameters r_d, G and r_n respectively (Table 6.1 and Figure 6.3).

The fecundity rates associated with Dwarfs and Normals respectively, r_d and r_n, are related to the size at spawning divided by the time (since recruitment) that they take to reach that size. The relative values of these parameters can, therefore, be estimated from field data (Appendix C). The recruitment factor, G, cannot be estimated from field data since it requires knowledge of the accumulated chance of mortality experienced by an individual as it grows from the egg to recruitment as a Normal. As discussed in Chapter 5, this kind of information is practically impossible to obtain from a natural system. The modelling approach nevertheless allows this parameter to be varied over a wide range of values in order to examine its influence on the system.

Despite not being able to estimate G from a natural system, the direction of change of its value as environmental conditions vary can be ascertained. A high value of G implies that many individuals survive to recruitment. In a size-structured population this means that G is closely associated with the growth rate in Habitat 1. As a first approximation, high growth rate implies high G since it will reduce the time and hence accumulated chance of mortality taken to reach threshold recruitment size. Whilst this approximation may be valid for Dwarf/Normal systems, a number of other factors, such as mortality vs. growth rate trade-offs and seasonality, serve to complicate this relationship meaning that care must be taken in transferring this tentative relationship to analogous systems such as smolting salmon (e.g. Hutchings & Myers 1994)

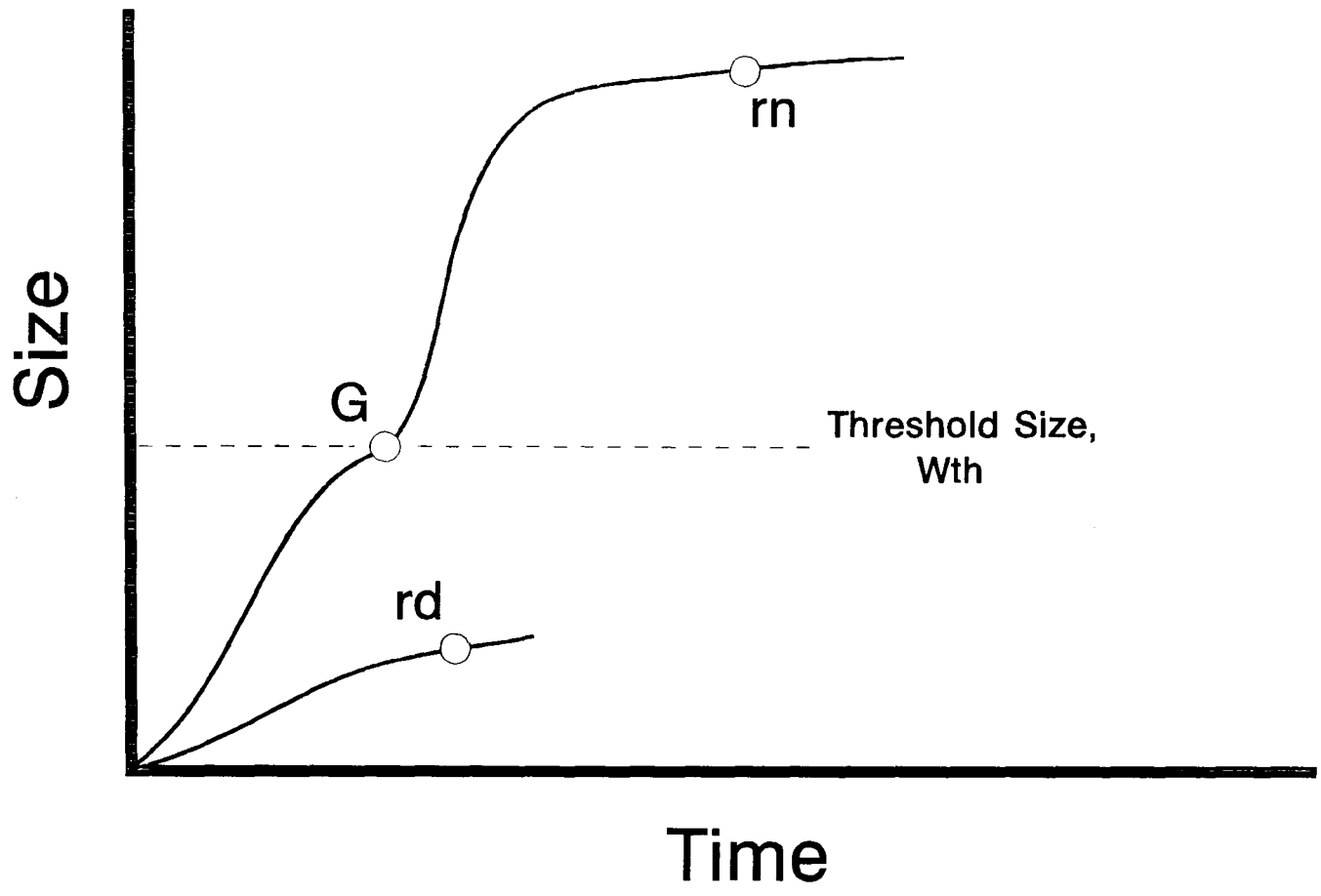


Figure 6.3 Parameterisation of optimised Dwarf and Normal Life History Strategies. r_d, r_n represent fecundity at optimal age and size at maturity for Dwarfs and Normals respectively. G is the optimised parameter which measures the mortality penalty associated with the Normal strategist reaching the Dwarf/Normal size threshold.

6.3.2 Competition and density dependence

Unlike the model of Chapter 5, where the individual was subject to abstractly-defined but constant energetic constraints and trade-offs, the individual in Chapter 6 is considered as part of a population. This means that the constraints on the individual are affected by the other members of the population through the mechanism of competition. In turn, this implies that values of the optimised parameters will be affected by the population dynamics.

Three terms of the model simulate these aspects of competition as well as serving other purposes. The $\text{Exp}(-(D+J)/K_d)$ and $\text{Exp}(-N/K_n)$ terms mimic the decrease in fecundities and growth rates at high population densities. They are, however, also intended as a crude representation of the negative frequency-dependent success of alternative reproductive strategies due to behavioural interactions on spawning grounds (Hutchings & Myers 1994, Gross 1984); as well as another behavioural interaction whereby recruitment to both habitats is limited by the density of individuals already within it (Johnson's 1976 "filter"). Alternative density-dependent functions of the form $(K_d / (K_d + D + J))$ and $(K_n / (K_n + N))$ were also tried without materially effecting the behaviour of the models.

The third competition term is $J/(D+J+D_o)$ which models the competition between the strategies in $H1$. Density-dependence is envisaged to limit growth rate and, hence, the presence of Dwarfs in $H1$ will reduce the ability of Juvenile Normals to reach critical size and recruit to $H2$. The term can also be seen as the proportion of $H1$ which is available to the Juvenile Normals. D_o is small relative to the equilibrium values of D and J and limits recruitment to biologically-sensible finite limits at low values of $D + J$.

6.3.3 Evolutionarily stable strategies (ESS)

An "evolutionarily stable strategy" (ESS) is defined as a strategy such that, if most members of the population adopt it, there is no mutant strategy that would give higher reproductive fitness (Maynard Smith & Price 1973). A mixed strategy is an ESS where

more than one strategy coexists at a defined frequency. In the Dwarf/Normal system there are two ways in which a mixed strategy can be implemented, and it is impossible to distinguish between the two just from knowledge of the mixed strategy frequencies. Paraphrasing Maynard Smith 1989 (p129):-

a) If only pure strategies are possible, the population will consist of, say, 1/3 pure Dwarf and 2/3 pure Normal. This is the separate stocks model.

b) If individuals can adopt mixed strategies, the population will come to consist of mixed strategists, "playing" Dwarf or Normal with probabilities of 1/3 and 2/3 respectively. This is the single stock model.

Some less essential aspects of the model are deferred to further appendices. Appendix D is an example of a template from the software package SOLVER which was used to analyse the models. Appendix E is the MATLAB program used to analyse the transient behaviour of the models close to equilibrium. Appendix F describes the formulation of stage-structured models which incorporate developmental delays. Whilst more realistic, these models are harder to analyse and are used as a sensitivity analysis to validate the results generated predominantly from simpler models which themselves neglect development time.

6.4 Results

Results are presented along with their relevance to direct observation as follows:-

- An analysis of the equilibrium conditions as the recruitment factor, G, is varied.
- The conditions for generation of unimodal (stunted) populations.
- The evolutionarily stable (ESS) form of the "weighted coin" in the single stock model as recruitment factor, G, is varied. (Model B)
- The outcome of the speciation model (Model C) when pure strategists and mixed strategists compete within stable and fluctuating environments.
- A sensitivity analysis of the dynamic response characteristics of the two models.
- A sensitivity analysis using models which incorporate time delays.

6.4.1 Equilibrium conditions vs. recruitment factor, *G*

It was argued previously that the equilibria associated with both Models A and B will be the same for any given set of model parameters providing that both models exhibit an ESS. Thus, it is possible to conduct an analysis of equilibrium conditions without knowledge of the "weighted coin". Figure 6.4 illustrates the different equilibrium regimes calculated using Model A as the absolute values of the fecundity terms, r , are varied in the observed ratio of 1:4 while other parameters remain at default settings (Table 6.1). Figure 6.5 shows the actual variation in sub-population numbers through a "cross-section" of Figure 6.4 as the recruitment factor, G, is varied. There are regimes of "Dwarfs only", coexistence and "Normals only".

In Dwarf/Normal systems, large G is argued to be associated with high growth rate in Habitat 1. The figures therefore make two predictions which agree with observation. First, all-Dwarf populations are associated with low G and this compares with the slow growth that gives "stunted" populations their name. Second, high G, and hence good growth conditions, is associated with large numbers of Normals. Whilst still remaining speculative, this result adds credence to the assertion that these two features of a population may be related (Chapter 4, Question 3).

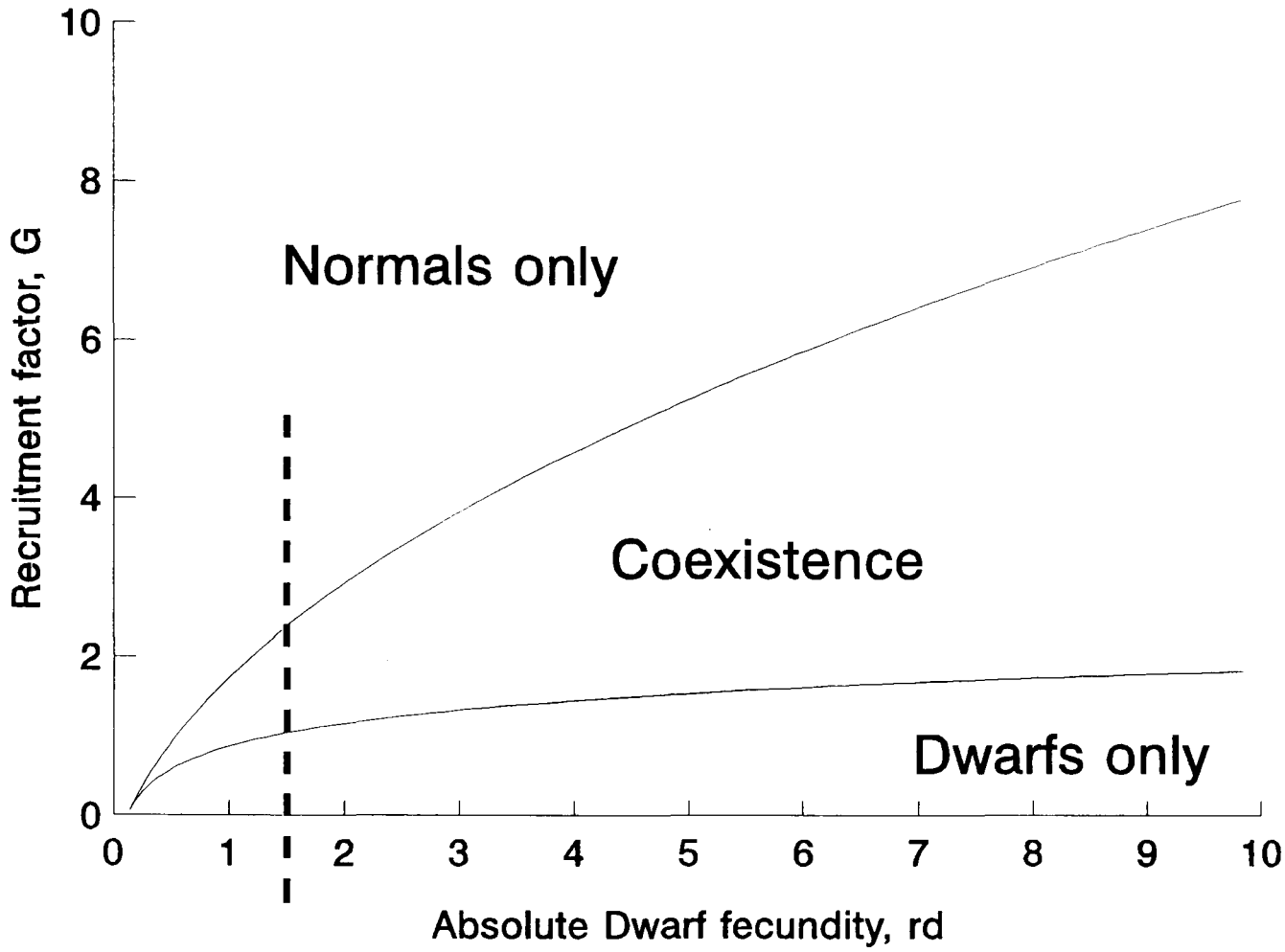


Figure 6.4 Result of analysis showing conditions for existence of Dwarfs and Normals at equilibrium as environmental conditions change. There are regimes of "Dwarfs-only", coexistence and "Normals-only" as absolute values of fecundity r_d and r_n are varied. The ratio of Dwarf to Normal fecundity is maintained constant at 1:4 to reflect observation. The vertical dotted line represents the parameters analysed in more detail in Figure 6.5.

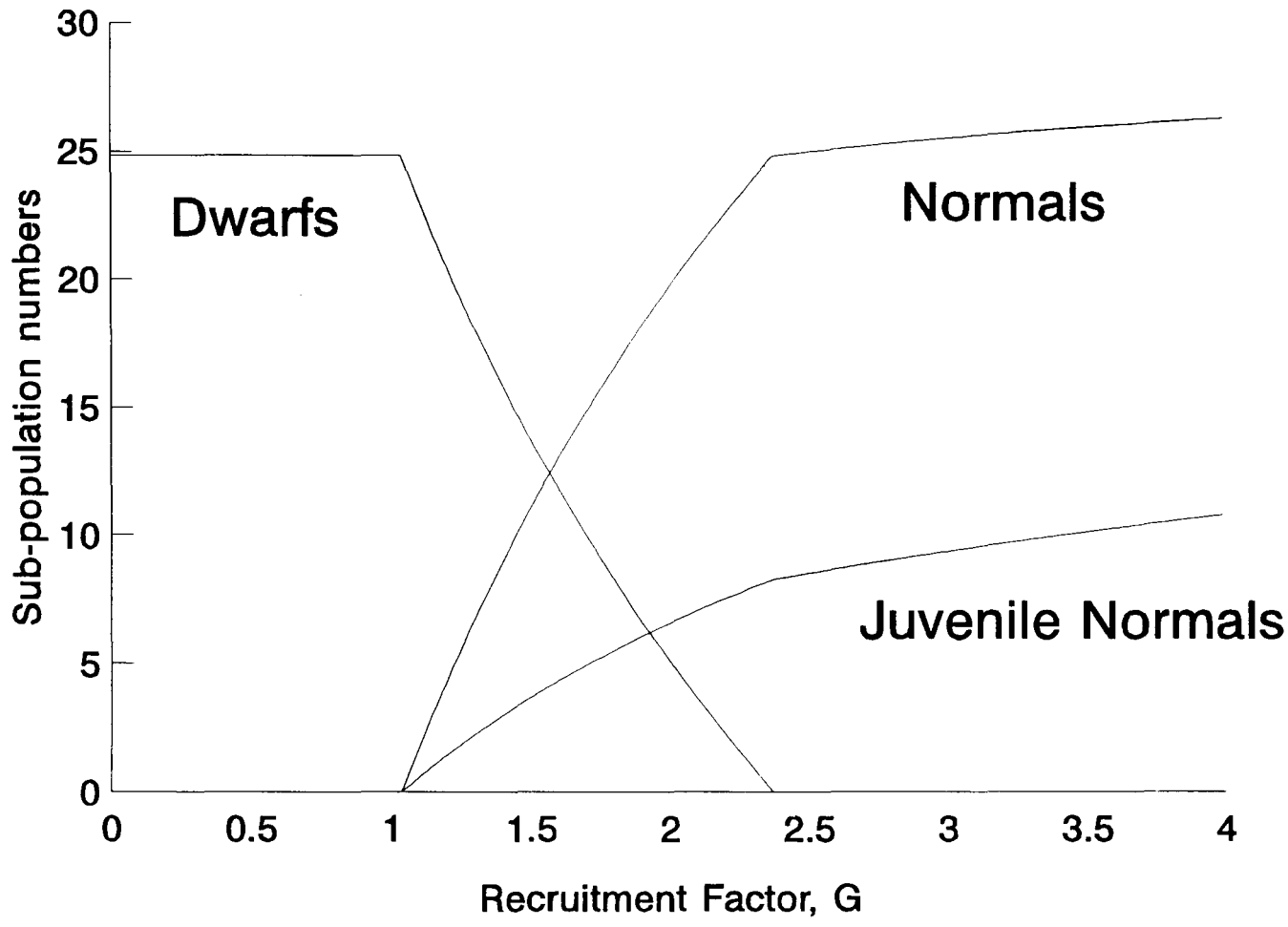


Figure 6.5 Actual sub-population equilibria as recruitment factor, G, is varied while other parameters remain at default values (Table 6.1). This diagram provides the detail for those parameters marked with a dotted line in Figure 6.4.

6.4.2 Conditions for stunting

Transition between model regimes for the separate stocks model occurs at analytically calculable values of G. The boundaries are:

Between "Dwarfs only" and coexistence, $G = \mu_j . \mu_n . K_d . \ln(r_d / \mu_d) . r_d / (r_n . \mu_d - r_d . \mu_n)$

Between coexistence and "Normals only", $G = \mu_n . N^* / \exp(- N^* / K_n)$,

where $N^* . (r_n . \mu_d - r_d . \mu_n) = r_d . \mu_j . J^*$ and $J^* = K_d . \ln(r_d / \mu_d)$.

The condition for stunting is where the value of G falls below the boundary between "Dwarfs only" and coexistence. If the further approximation is made that $\mu_j = \mu_d$ then this boundary can be rewritten as: -

$$G_{stunt} = K_d . \ln(r_d / \mu_d) . r_d / (r_n / \mu_n - r_d / \mu_d)$$

Figure 6.6 illustrates how G_{stunt} might vary as the ratios of r/μ for the two habitats are varied against each other. From this it is apparent that the greater the difference between r/μ, the greater the numbers of Normal fish. r_n / μ_n must be greater than r_d / μ_d and if they ever become equal stunting will always occur.

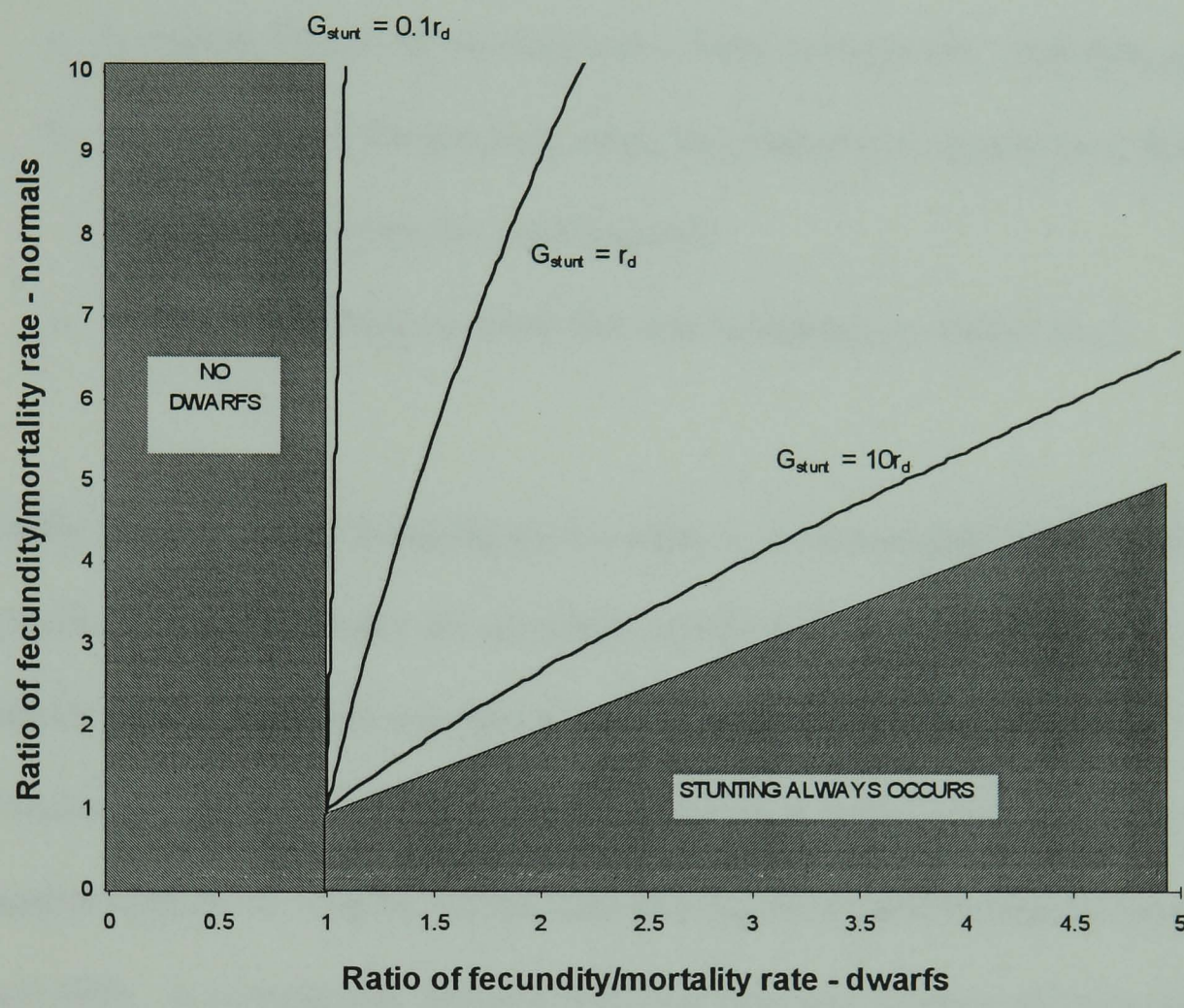


Figure 6.6 Conditions for stunting as a function of differences in the ratio of fecundity to mortality rate between Dwarfs and Normals. The important points are that if $r_d/\mu_d > r_n/\mu_n$ then stunting will always occur; and that the condition for stunting becomes easier to overcome the larger that r_n/μ_n becomes relative to r_d/μ_d.. A stunted population is unimodal consisting entirely of slow-growing dwarfs.

The practical importance of Figure 6.6, if maintenance of bimodality is considered desirable, is that management practice must be aimed at preserving or increasing the difference in the r/μ ratio. This could be achieved in a number of ways:-

a. In a sport fishery, by placing a catch limit on large fish. (reducing μ_n)
b. By reduction of the spawning area, thus reducing r_d relative to r_n through size-specific competition for spawning sites
c. By selective fishing on small fish thus increasing μ_d relative to μ_n.

Of the these means of managing the r/μ ratio, a. is increasingly becoming common practice although probably for unrelated reasons; b. is speculative in that no case is known where it has been attempted; and c. has been conducted in Takvatn, Norway (Amundsen 1989). In this experiment, funnel traps, which select for small fish, were used to remove 13.1 kg/ha. of fish from this typical stunted population between 1984 and 1986. A considerable increase in growth rates and numbers of large charr have been observed since.

6.4.3 The evolutionarily stable (ESS) form of the "weighted coin" in the single stock model (Model B) as a function of recruitment factor, G.

If it is assumed for the single stock model (Model B) that the "weighted coin" which determines the choice of life history strategy is itself subject to natural selection, an analysis can be made in which individuals adopting different "weighted coins" compete within the same lake. The ESS will be represented by the individuals which adopt the "weighted coin" which outcompetes all the other possibilities.

Suppose that the lake is occupied by two competing single stock models (Model B's) in which one model consists of Dwarfs, Juvenile Normals and Adult Normals labelled *D, J, N* whilst the other is labelled X,Y, Z. By analogy with Table 6.2, and without presenting all the equations, the situation is illustrated by:-

$$\frac{dD}{dt} = p_d.(r_d.D + r_n.N).\exp(-\frac{(D+J+X+Y)}{K_d}) - \mu_d.D \qquad \text{Eqn 1}$$

$$\frac{dX}{dt} = p_x.(r_d.X + r_n.Z).\exp(-\frac{(D+J+X+Y)}{K_d}) - \mu_d.X \qquad \text{Eqn 2}$$

etc.

At equilibrium, $\frac{dD}{dt} = \frac{dJ}{dt} = \frac{dN}{dt} = \frac{dX}{dt} = \frac{dY}{dt} = \frac{dZ}{dt} = 0$ (6 equations)

and, if $p_d = r_d.D^*/(r_d.D^* + r_n.N^*)$, note [6]

[6] Standard notation is followed. D* means "the equilibrium value of D"

Eqn 1 implies $$\exp\left[-\frac{(D^* + J^* + X^* + Y^*)}{K_d}\right] = \frac{\mu_d}{r_d} \quad ,$$

Substitution into Eqn 2 and further simple substitutions into the remaining equations gives the following cases which can satisfy the six simultaneous Differential Equations at equilibrium:-

Case I: $p_x = r_d \,.X^* / (r_d.X^* + r_n \,.Z^*)$ ie X, Y, Z identical to D, J, N

Case II: $X^* = Y^* = Z^* = 0$ ie X, Y, Z extinct

Case III: $p_x = 1$ and $Y^* = Z^* = 0$ ie some pure Dwarf strategists can coexist with the mixed strategist

Case IV: $p_x = 0$ and $X^* = 0$ ie some pure Normal strategists can coexist with the mixed strategist

In words, if an individual adopts a mixed strategy then the ESS value of the weighted coin is $p_d = r_d \,.D^* / (r_d.D^* + r_n.N^*)$. Any other value for the weighted coin leads to extinction of the genotype adopting it. A further possibility is that the population will consist of an undefined mixture of Dwarf and Normal pure strategists plus some mixed

strategists. In this way the single stock model (Model B) can coexist with the separate stocks model (Model A) providing that the model assumptions of a stable environment, equal fecundities, r, and equal death rates, μ, hold. These conclusions are supported by substitution of relevant trial values for the weighted coin into the model.

It was shown in section 6.4.1 that the equilibria vary as a function of G. It is thus a simple matter to calculate p_d over all values of G. This is illustrated at Figure 6.7.

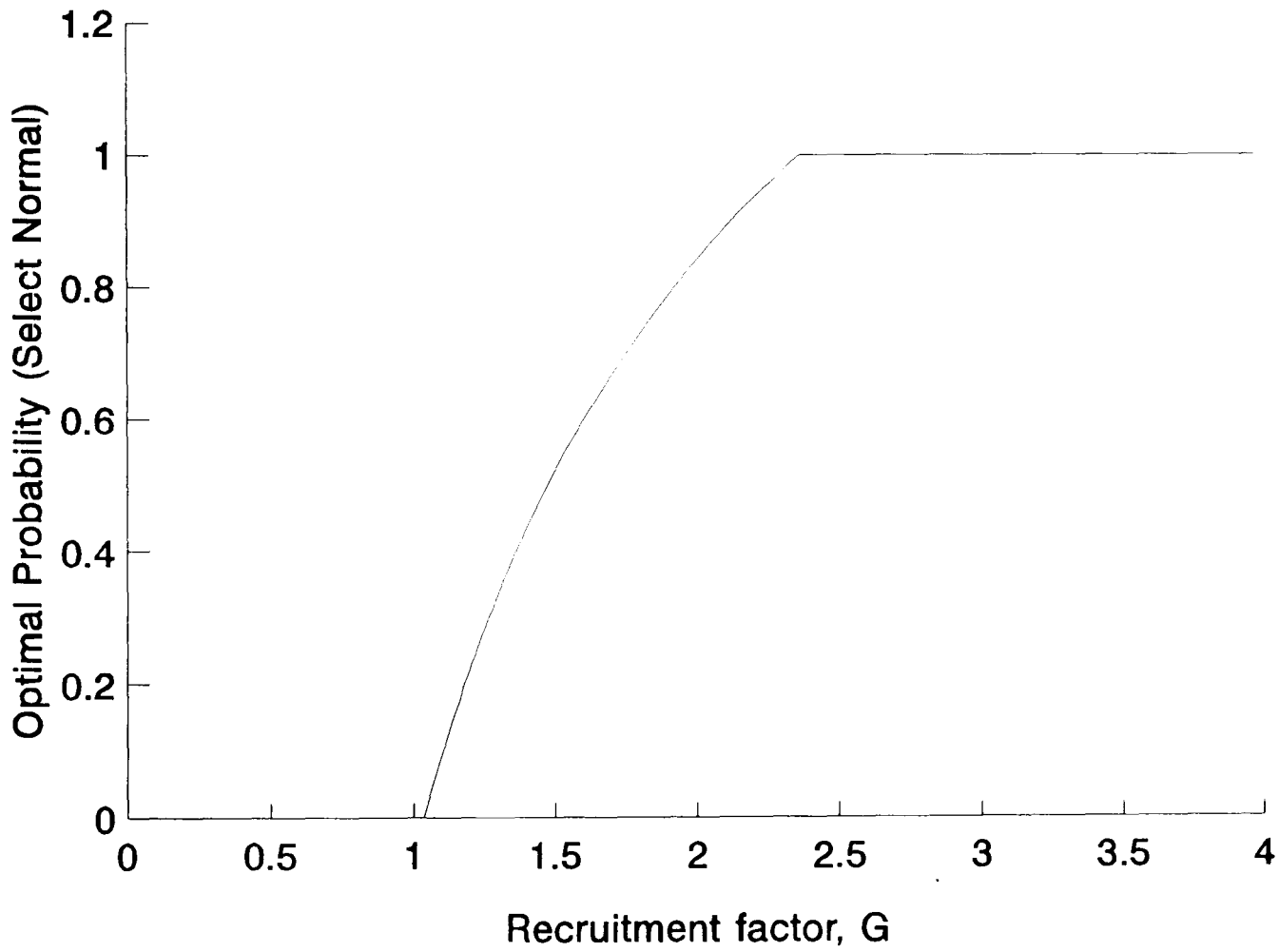


Figure 6.7 The Evolutionarily Stable "weighted coin" for the single stock model as a function of recruitment factor, G. Only pure Dwarfs or pure Normals are able to compete successfully with an individual using this coin. The "weighted coin" is the reaction norm by which an individual chooses life history strategy.

Unfortunately, little work on life history responses to growth stimuli has been reported for Arctic charr but experiments with smolting in Atlantic salmon provide a good comparison. Thorpe *et al.* (1989) showed that the percentage of smolts at age 1 was correlated with an "index of growth opportunity" during the July post hatching. The "growth opportunity" is analogous to the Recruitment Factor, *G*. The Thorpe *et al.* (1989) data show a threshold "growth opportunity" necessary before any individuals opts for smolting in year 1. This is followed by an approximately linear relationship of greater probability of smolting against further growth opportunity.

Comparison between Thorpe *et al.*(1989)'s results and Figure 6.7 reveals that they are similar functions. Thorpe's "growth opportunity" threshold may therefore be a result of selection due to the low likelihood of immediate success of the smolting strategy at low growth rates. Via & Lande (1985) discuss the genotype-environment interactions which might drive selection for an optimal phenotypic switch of this type.

6.4.4 Speciation model (Model C)

In order to tackle the unresolved question of the genetic relationships between life history strategies, both the separate stocks and single stock models are set into competition within the same habitats. This is best visualised by imagining that Figures 6.1 and 6.2 have been combined into one model in order to find which of Model A and Model B is the ESS (c.f. Section 6.4.3 which replicated this process using two Model B's with

different "weighted coins"). In a static environment, with fecundity and mortality rates equal, both models coexist neutrally (Section 6.3.3).

The imposition of environmental fluctuations onto the population reverses the above result and is implemented in modelling terms by driving all or one of the parameters K_d, K_n and G over a range of sinusoidal frequencies. Trial experiments using step changes in K_d, K_n and G were also conducted without effecting the end result of the model runs. This shows that, despite the non-linearities, the response to sinusoidal fluctuations is a fair indication of the model behaviour under the majority of conditions. The results of fluctuating the environment are most apparent when G is varied. In contrast to the steady state, the separate stocks are driven extinct under a wide range of circumstances.

Figures 6.8a. and b. illustrate the persistence times of the separate stocks model in competition with the single stock model assuming both types have the same fecundities and using default parameters (Table 6.1).

Mathematically, it is thought that the reason for this result is that the response time near equilibrium is much faster for the single stock model than for the separate stocks model and Figure 6.9 is the results of a sensitivity analysis which shows that the single stock model has faster response times around equilibrium whatever the value of G. This means that, in a variable environment, the single stock model will always be the ESS even though the value of G is not known.

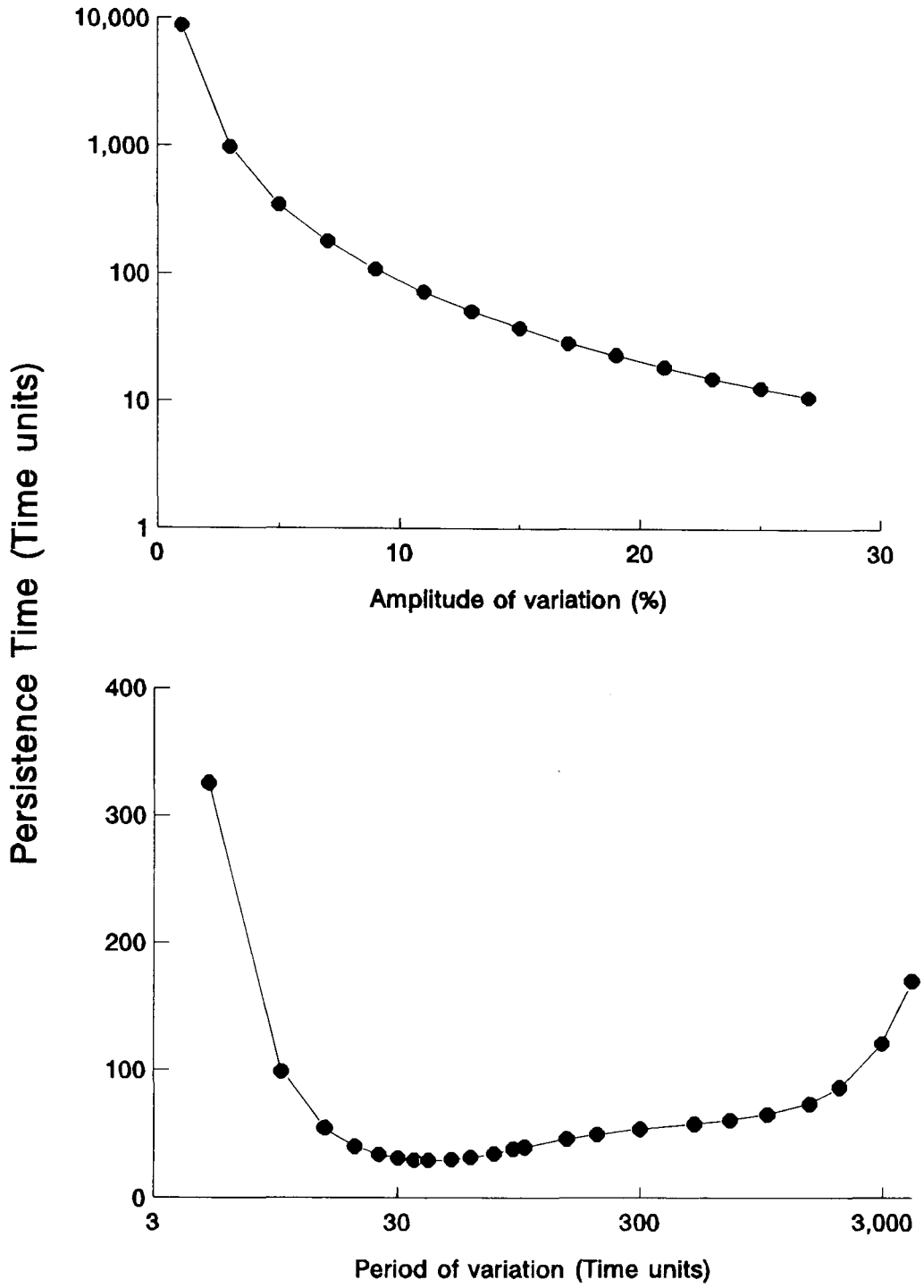


Figure 6.8 Persistence times for the separate stocks model in competition with the single stock model whilst subject to sinusoidal fluctuation in the recruitment factor, G. The upper diagram shows persistence as the amplitude of perturbation is varied with period fixed at 40 time units. The lower diagram shows persistence as the period is varied with the amplitude set at 10%. Persistence is defined as the time for both separate stocks Dwarfs and Normals to fall below a fixed low level. Both diagrams were calculated using default parameters.

Biologically, the reason for this result is that the fitness of an individual is determined by the average success of its offspring. In a fluctuating and unpredictable environment, it is a better strategy for the individual to "bet-hedge" by having some offspring of each type. This is illustrated by the extreme case where, say, the Dwarfs become extinct. In the single stock case, the strategy can be resurrected from Normal offspring. In the separate stocks case, there is no means for the strategy to be re-established.

6.4.5 Sensitivity analysis I - Dynamic response characteristics of the models

Figure 6.9 is a summary of the dynamic characteristics of the separate and single stock models as G is varied whilst the other parameters remain at their default values. Mathematically, the diagram shows the negative real part of the dominant eigenvalues of the stability matrices linearised about equilibrium and the MATLAB program used is at Appendix E. The fact that positive real roots are never achieved indicates that both systems are always stable. Analysis (not illustrated) also indicated that there is no imaginary part to the dominant eigenvalue indicating that both systems return to equilibrium without oscillation. The importance in this context is that the larger the negative real part, the faster the system response time. It is shown that the single stock model retains fast response times relative to the separate stocks model throughout.

At risk of presupposing the single stock result, the single stock characteristics reflect one of the features of Arctic fish populations which is their long-term stability in the face of environmental variability experienced over their recent history (c.f. Section 2.5.2). This

has been demonstrated in previously undisturbed Arctic charr systems by removal of the Normals and monitoring the return to equilibrium over a 15 year period (Johnson 1994). The return to equilibrium was both rapid and without apparent oscillation. It would be revealing to conduct a comparative experiment in a system where charr interact with another species.

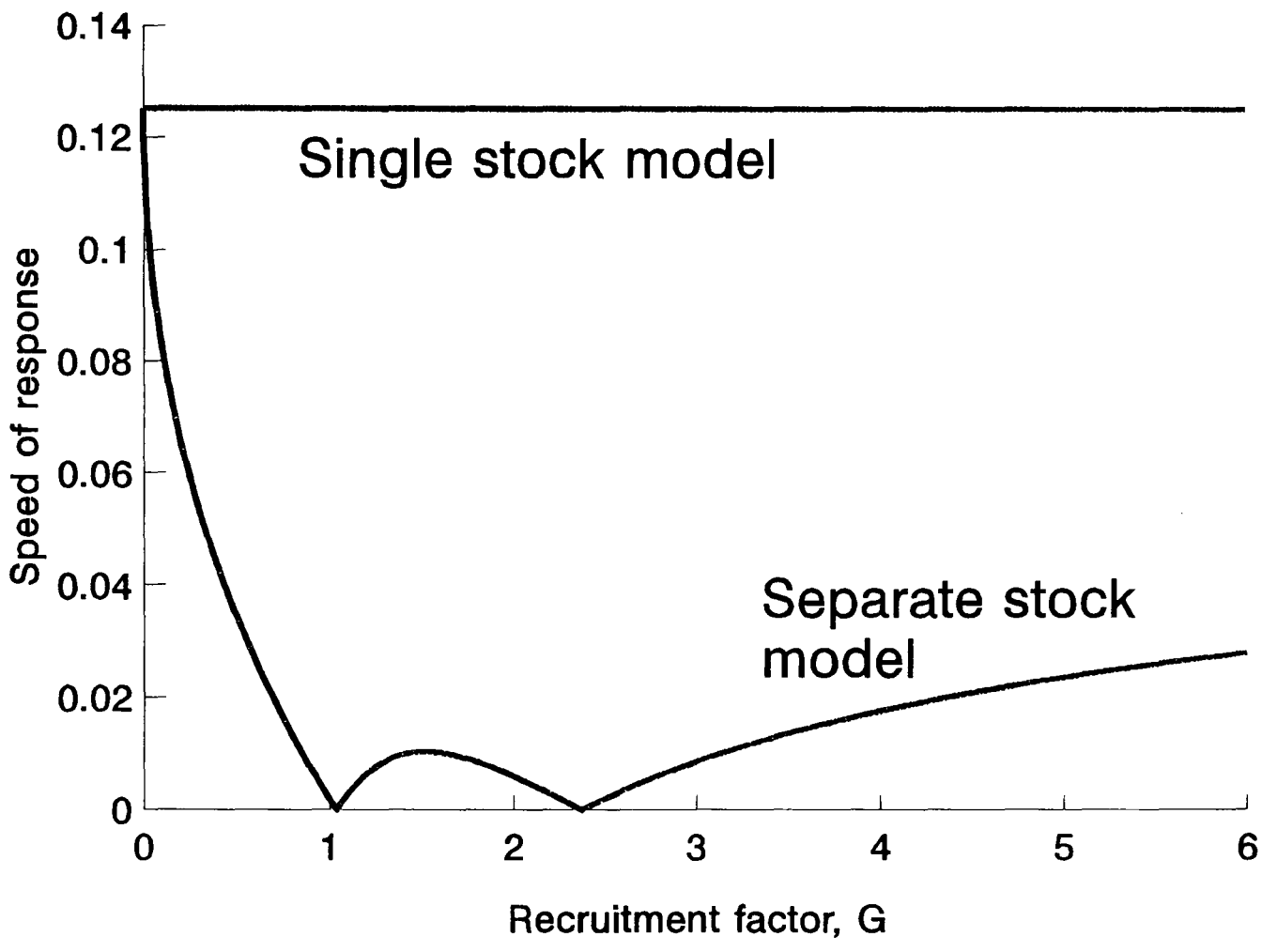


Figure 6.9 Speed of Response diagram. Mathematically, the y-axis is the negative real part of the dominant eigenvalue of the linearised stability matrix at equilibrium. Biologically, this means that the single stock model has a faster response time throughout the model range.

6.4.6 Sensitivity analysis II - Incorporation of time delays

The models used so far are termed unstructured because they have neglected the effects of time delays. The advantage of these models is that they are simpler and analytically more tractable than structured models, which include time delays. A comparison between unstructured and stage-structured models (Appendix F) is desirable to confirm that the results are not merely a result of over-simplification. The main points from the unstructured models are that equilibria are the same for both models for any given set of environmental parameters K_d, K_n and G; and that the single model has faster response times near equilibrium. Figure 6.10 shows time responses for all four models at default parameters when a small number of individuals are introduced at time, $t = 0$, to a system of fixed carrying capacities, K.

It is noted that:

a. All models reach equilibrium at similar steady state values for Dwarfs, Juvenile Normals and Adult Normals. This has been achieved by the calculations of Appendix C, where the unstructured model parameters are scaled to allow for the additional mortality experienced in the stage-structured models during the immature stages. This means that transfer of the equilibrium analysis and the general results about stunting is valid.

b. The differences in response times are even more apparent in the stage-structured than the unstructured models in that the stage-structured Model A is slow to reach equilibrium relative to Model B. This indicates that the argument on dynamic characteristics is more rather than less relevant when developmental delays are taken into consideration. The single stock model will therefore drive the separate stocks model to extinction relatively even faster than in the unstructured case. This was confirmed by sample runs of a stage-structured version of the speciation model.

c. The oscillations initially apparent in the stage-structured models have no biological significance other than that they take longer to damp out in the separate model. They are due to the lack of knowledge of the population status prior to $t = 0$, but the inherent stability of both models allows each population to find its own equilibrium without massive fluctuations.

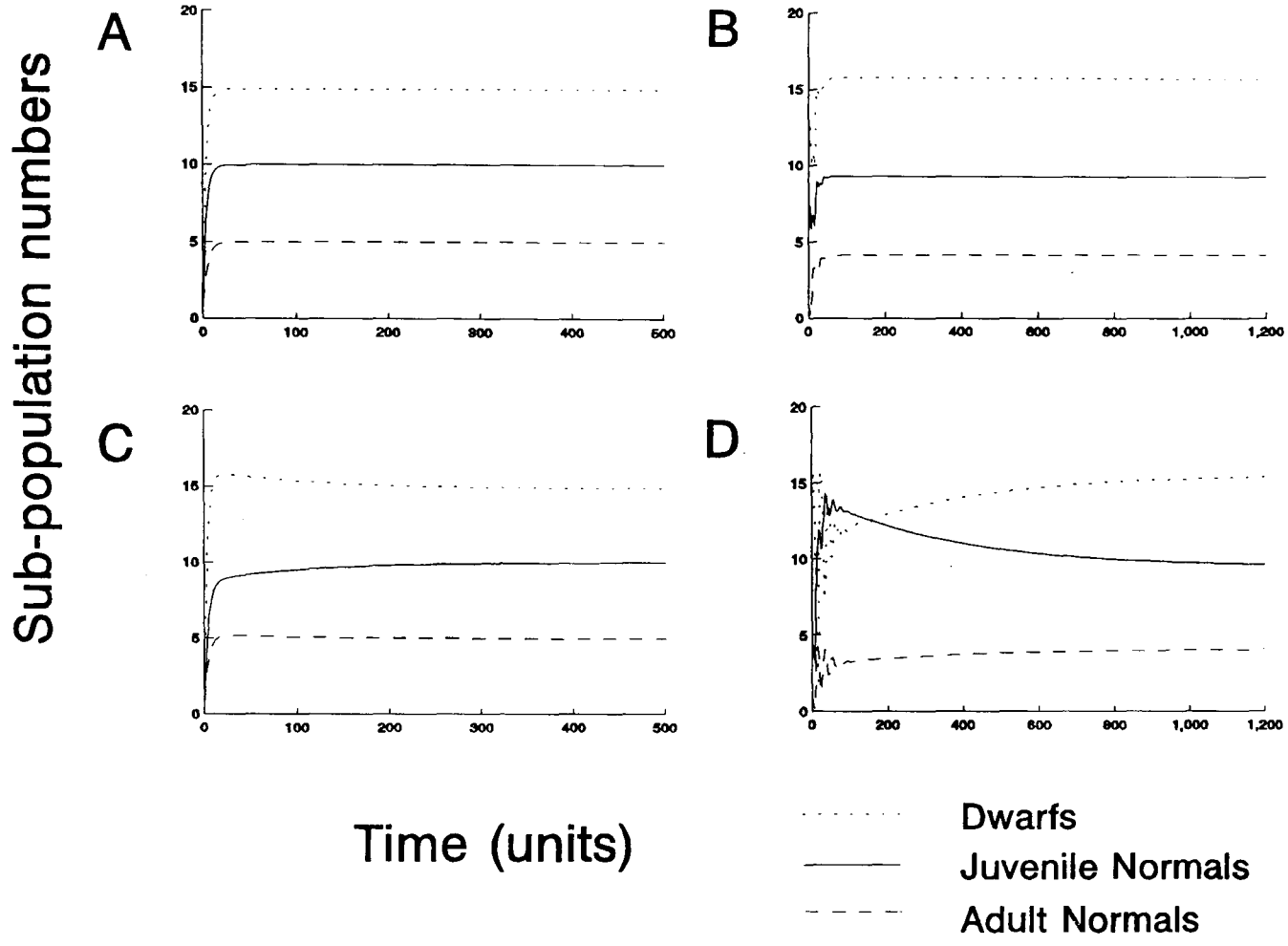


Figure 6.10 Sub-population numbers against time for small numbers of individuals introduced to a system of fixed carrying capacities:-

A. Single stock model neglecting development times (Unstructured).

B. Single stock model incorporating developmental delays (Stage-structured).

C. Separate stocks model neglecting development times (Unstructured).

D. Separate stocks model incorporating developmental delays (Stage-structured).

6.5 Discussion

6.5.1 Population structure

The main findings on population structure are that, in stable environmental conditions:-

- The population structure is independent of the means by which life history strategy is chosen so long as the means achieves ESS proportions of Dwarfs and Normals (Section 6.3.3).

- If the ESS includes both Dwarfs and Normals both strategies are equally fit at equilibrium (Chapter 4 Question 2).

- A high proportion of Normals is thought to be associated with high growth rate as a juvenile; and a "stunted" or unimodal population with low growth rates (Section 6.4.1). (Chapter 4 Question 3).

- A difference in the ratio of fecundity to mortality rate (r/μ) between Dwarf and Normal sub-populations is essential to maintaining bimodal populations (Section 6.4.2).

- The predicted ESS for selection of the Normal strategy is similar to that observed experimentally for smolting in Atlantic salmon (Section 6.4.3, Figure 6.7)

Cannibalism as a regulatory mechanism

Experimental evidence mainly in other species (e.g. Werner *et al.* 1983, Gilliam & Fraser 1987, but also Damsgård 1993) suggests that cannibalism, or the threat of cannibalism, by Normals upon Dwarfs would:-

a. invoke a behavioural response amongst Dwarfs which would reduce their growth rate.

b. provide an alternative source of food for Normals which would increase their growth rate.

c. increase the mortality rate on Dwarfs.

(d. decrease the mortality rate on Normals.)

Given that fecundity is closely related to size, growth rate and fecundity rate are also related. Hence, cannibalism will increase the ratio of r/μ for Normals whilst reducing it for Dwarfs. By the findings on population structure above, this means that there are good theoretical reasons for why cannibalism might be successful in maintaining bimodality. This has been speculated upon previously (e.g. Amundsen 1989) but not on theoretical grounds. It is emphasised that cannibalism is not the only way that bimodality can become a feature of populations (Huston & deAngelis 1987)

6.5.2 Potential speciation

The speciation model (Model C) illustrates that the separate stocks model can be excluded by the single stock model if there is enough environmental variation at adequately high frequency. The long term result does not appear to be affected by the magnitude of the perturbations, indicating that over evolutionary time only slight fluctuations are adequate to maintain the single stock model as the ESS. Without modification to the model, this indicates that there is no adaptive advantage to the separate stocks model and speciation will generally not occur. This has important implications to Chapter 4 Question 2 since now the fitter individual is neither pure Dwarf nor pure Normal but one which, partly via its offspring, retains the ability to do both.

"Specialists" versus "Generalists"

Considerations of speciation become more revealing, however, if it is supposed that the common gene pool of the single stock model limits the degree of adaptation which can be achieved within each of the habitats; and that reproductive isolation might lead to greater adaptation as a "specialist" in one or other of the habitats. In this case, the single stock model would represent a "generalist" strategy, whilst the separate stocks model would represent a "specialist" strategy.

The increased habitat-specific adaptation associated with specialisation can be modelled as a slight increase in r/μ for the separate stocks (Model A) relative to the single stock

(Model B). In the steady state, with no simulation of environmental variation, this assumption leads to total extinction of the "generalists". If environmental variation is added however, there is a situation where the dynamic characteristics of the model (section 6.4.4) cancels the tendency in the steady state for "specialists" to exclude "generalists". This leads to the conclusion that a compromise occurs, at some point between the single stock and separate stocks models, which achieves maximum individual fitness. In this state of "semi-speciation", some adaptive advantage can be achieved as a "specialist" without totally excluding the ability to "play the other strategy", albeit to some small disadvantage, if circumstances require.

Genetic polymorphism

Experimental evidence for smolting in Arctic charr (e.g. Nordeng 1983, Nordeng *et al.* 1989) or Atlantic salmon (e.g. Metcalfe *et al.* in press) suggests that there is at least some genetic component to smolting and, by analogy, this is probably also the case in the Dwarf/Normal system. This has some importance to the assumption of the "weighted coin" in the single stock (Model A) since the model assumes that it is achieved within a random mating population. Considerable theoretical work of a general nature (e.g. Levene 1953, Maynard Smith & Hoekstra 1980, Hoekstra *et al.* 1985, Hedrick 1986) asks whether genetic polymorphism can be achieved in a random mating population.

The results of this work indicate that the conditions for achieving a genetic polymorphism within a random mating population are tight and unlikely to be realised in a charr system without the relaxations of "habitat selection", whereby offspring utilise the maternal patch type rather than being randomly distributed; or "mating within a patch", with different degrees of assortative mating (Maynard Smith 1989 p75). It can be speculated that both these relaxations occur. Large fish lay larger eggs (Chapter 2) and this correlates with faster initial growth (Sargent *et al.* 1987, Wallace & Aasjord 1984) and more Normals (Chapter 5) thus achieving "habitat selection". Similarly incomplete assortative mating is a common feature of most Salmonid populations (e.g. Jonsson & Hindar 1982).

That the mixed ESS may be associated with these relaxations in some natural systems does not, however, necessarily mean that it could not exist without them. The Takvatn experiment (Amundsen 1989), for example, illustrates that a bimodal population can be regenerated from a stunted one without a contribution from a Normal sub-population. The "weighted coin" is therefore almost certainly a fundamental property of individuals in nature as well as in the model. The only way to find out for certain may be to repeat Thorpe *et al.* 's (1989) experiments with clonal fish (c.f. Weeks & Quattro 1991) with respect to life history plasticity in growth and reproduction).

It is thus likely that the means of achieving the mixed ESS in nature varies with local conditions. Where genetic differences between sub-populations occur it is thought that assortative mating is important in maintaining an interim configuration between the separate stocks (Model A) and the random-mating single stock (Model B). This interim

configuration reflects the state of "semi-speciation" predicted to give greatest individual fitness in the natural system. Between the two extremes of the models lies an infinite number of possibilities, thus emphasising the potential flexibility of the mechanism to allow exploitation of a wide range of local conditions.

The "charr" problem

This chapter has some impact on the "charr problem" (Chapter 1) and the two main hypotheses which exist as to potential mechanisms for genetic divergence (Klemetsen & Grotnes 1980). The first of these mechanisms is allopatric speciation via successive reinvasion of the systems from different glacial refugia after the Pleistocene. The second is the mechanism of sympatric speciation, the credibility of which has recently been greatly strengthened by both theoretical work and experiment (e.g. Kondrashov & Mina 1986, Rice & Salt 1990, Rice & Hostert 1993, Bush 1994).

Inasmuch as incomplete assortative mating is an early stage in the process of sympatric speciation, this chapter might initially seem to favour sympatric speciation as the most likely mechanism. However, the chapter also indicates that full reproductive isolation can lead to reduced individual fitness if the environment is variable enough. If so, the population will not procede as far as speciation and incidence of genetic divergence will increase towards the more environmentally predictable southern extremes of the species range. (Chapter 4 Question 4).

7. Synthesis

Chapter 4 presented an overview of the most important aspects of the fieldwork and indicated four questions that demanded closer attention. The key hypothesis that the observations could be explained as a result of adaptation to energy limitation within a size-structured population was introduced, and the probable existence of a largely undetected mode of pelagic charr in one lake identified. This final chapter examines the success of the theoretical work in advancing understanding of the questions raised, and also raises a number of themes which connect otherwise disparate parts of the thesis together.

7.1 *Juvenile Growth Rate and Life History Strategy*

Q1. What is the a relation between growth rate as a juvenile and life history strategy?

Whilst emphasising that the key assumption of energy limitation is never proved, Chapter 5 argued that energy limitation must lead to trade-offs between growth, reproduction and survival. Given the further imposition of size-structure, it is argued that the fitnesses of the Dwarf and Normal alternative life history strategies are optimised by different processes. The Dwarf's by optimising age and size at reproduction within the one habitat; and the Normal's by minimising the mortality penalty imposed during growth to threshold recruitment size and subsequently optimising age and size at maturity

within the Normal habitat. The model illustrated that, by combining these arguments, the two life history strategies are optimised at different growth rates. The model does not indicate the physiological processes that cause this optimisation to occur, but reference is made to other work where this has been achieved.

7.2 Interactions between Models

Q2. Which is the fitter animal - Dwarf or Normal?

Whilst Chapter 5 looked at the optimal response by the individual in isolation, Chapter 6 looked at how individuals apply constraints upon each other through the mechanisms of density dependence and population dynamics. The models are thus inextricably related because the output of one will effect the input to the other. Phenotypic responses to environmental stress will almost certainly change the controlling rates of births, deaths and recruitment which define the population dynamics of Chapter 6; whilst the density dependencies of Chapter 6 will change the external constraints imposed on the individual in Chapter 5.

Chapter 6 showed that the result of this interaction is that there is only one optimal rate of production of Dwarf juveniles relative to Normal juveniles for each set of local

conditions. Regions of "Dwarfs only", coexistence and "Normals only" were found. Where both types coexist, this implies that they are equally successful, and this in turn is contrary to much biological debate centred on which of the strategies is the better. The anthropocentric view that regards the Dwarf as an inferior competitior is wrong and, indeed, there are circumstances in which the Dwarf is fitter than the larger Normals.

In this sense, the population model is a means of measuring fitness since, at equilibrium, the rate of increase of both types is zero. Many fitness optimisation calculations only take into account the immediate success of an allele, genotype or phenotype and this is the case in the model of Chapter 5. In the "steady state" this is a reasonable assumption, but in a variable environment the means by which fitness is being optimised is always changing. As a result, the population dynamic model is a better measure of fitness than optimisation since it is effectively calculating the average success of the spectrum of an individual's offspring over a large number of generations.

The argument of evolutionarily stable strategies (ESS's) as it relates to the single stock model (Chapter 6) also challenges the question of which of the strategies is "best". An individual equipped with the necessary "weighted coin" can opt for the Dwarf or Normal strategy dependent on environmental conditions. In stable environmental conditions, this offers no advantage over two coexistent pure strategists. In a variable environment,

however, Chapter 6 shows that the individual with a "weighted coin" is fitter than either pure strategist.

7.3 Growth Rate and Population Structure

Q3. Do good growth conditions during the juvenile stages imply that a greater number of Normal charr will exist within the population at equilibrium?

The model of Chapter 6 showed that population structure is sensitive to the rates of recruitment between Dwarf and Normal sub-populations. This was modelled by the "recruitment factor", *G*. By definition, *G* is increased by anything which improves the chance of recruitment from Dwarf to Normal; and it was argued in Chapter 6 that, in a size-structured population, this must be closely associated with juvenile growth rate. The somewhat unsurprising prediction was made that the greater the value of G, the higher the number of Normals. It is thus possible to relate high juvenile growth rates to high numbers of Normals in the population structure.

7.4 Environmental Heterogeneity

There are many factors which may cause G to vary between real natural lakes but one may be the availability of zooplankton as an alternative resource; and for which there is some indirect evidence within Lake H (Chapter 4). Zooplankton are available for a greater part of the year than the remainder of the small charr's food supply and may provide a means to maintain the necessary growth rates to surmount the critical threshold size needed for recruitment to the Normal sub-population. In this way, the zooplankton are providing the "energetic pathway" between Dwarf and Normal referred to in Chapter 4. It must, however, also be noted that the presence of a significant planktonic resource is not essential to population bimodality because there was little evidence of such a resource being available to the bimodal population of Lake C.

Feeding upon zooplankton is probably only the most important of a number of other possible "feeding specialisations" within each of the idealised habitats of Chapter 6. The evidence for feeding specialisation within the survey was slight (Chapter 2), but this was only over the brief summer sampling period. The dispersion in the parasite infections (Chapter 3) implied that heterogeneity in feeding tactics is, by contrast, a common feature over all the apparently homogeneous habitats encountered. Work by Amundsen (Amundsen & Klemetsen 1986, Amundsen *in press*) also shows that there is considerable individual variation in stomach contents, not only by quantity but also by type of prey, in similar systems in Norway.

7.5 Maintenance of Population Structure

A key insight from Chapter 6 is that the ratios of fecundity rate to mortality rate (r/μ) are vital to maintaining bimodal population structures. In particular, if r/μ is greater for the Dwarfs than for the Normals then a bimodal population cannot be maintained and a "stunted" unimodal population will occur. This result correlates with the conditions for niche shifting in the theory of size-structured populations (Werner *et al.* 1983). In this case, the theory supposes that an individual should shift when the ratio of growth rate to mortality rate is equal in both habitats. Given that growth rate and fecundity rate are closely associated due to the relation between body size and fecundity, this is a sensible result.

The potential for cannibalism to assist in maintaining bimodal population structures was discussed in Chapter 6 on the basis that the behavioural interaction between prey and predator may result in the necessary difference in the r/μ ratio. There is some support for this theoretical prediction from Chapter 3, where cannibalism by a sub-group of Normals might explain certain aspects of the pattern of parasite distributions in the populations of Lakes C and H. In addition, cannibalism was occasionally observed and Normal charr appear morphologically adapted as piscivores. Other than the model, however, there is no necessary causality between cannibalism and the population structure.

7.6 Potential Speciation

Q4. Are the different size modes of charr within each lake genetically divergent? If so, what is its ecological significance and how is the divergence maintained?

This question was tackled in Chapter 6 by using models representing two extremes. The separate stocks model assumed that Dwarfs and Normals were separate species; the single stock model assumed a common gene pool. It was also assumed that the common gene pool limits the degree of specialisation that can be achieved within each of the separate habitats.

It was shown that the main disadvantage of specialisation in the variable environment is that an individual in one habitat is not able to exploit the other habitat (in some cases via its offspring) if conditions within it become more favourable. This is manifested in the population dynamics by the much slower return to equilibrium exhibited by the separate stocks model relative to single stock model (Figure 6.9).

The mechanism for selecting ESS proportions of offspring in the single stock model was presumed to be a "weighted coin" and the predicted function (Figure 6.7) was similar to that shown experimentally by Thorpe *et al.* (1989) for probability of smolting vs. growth opportunity in Atlantic salmon. If the connection is allowed between growth rate and G, this shows that juvenile growth rate is a good predictive stimulus on which an individual

might base its "choice" of life history strategy and, thus, that the form of the function not only exists in nature but has probably been selected for.

The model concluded that average individual fitness is optimised within the population as a whole in a "semi-speciated" condition. Incomplete assortative mating was argued as being important in maintaining this state. The conclusion that "semi-speciation" is the optimal configuration is an example of "selection for variation" at its crudest level. The importance of heterogeneity within the two idealised habitats of the population dynamics model has, however, already been discussed with respect to the "recruitment factor", G. It is likely, therefore, that there is a significant number of subtle variations upon the two habitat model assumed. In reality there are probably two groups of habitats with similar properties, within which there is probably scope for further individual variation.

This selection for variation brings into question the validity of the traditional taxonomic approach to the problem of species in the case of Arctic charr. Savvaitova (1984) illustrates the problem with a bewildering list of different subspecies and different workers' views on classification. She also confirms that the problem has been known for some time and quotes Regan (1926, p.75) in "Organic evolution" who states "Once you begin giving specific names to lacustrine forms of char you never know where to stop". Twenty nine different "species" of Arctic charr have, at one point or another, been identified in Europe alone (Savvaitova, in press).

Three conclusions from Savvaitova (in press) are presented in full:-

"Most of Arctic charr forms are not species *in statu nascendi*. Often the complicated species structure doesn't necessarily reflect process of speciation and represents a quasistationary state of the interrupted divergence which is able to reverse."

"Such complex structure of species has an adaptive significance and it enhances homeostasis (tendency towards stable equilibrium) in the oscillating environment in extreme conditions. It is rather common in other groups of fishes in high latitudes."

"The concept of a species complex is more applicable for classification of such structure."

The importance of the population dynamic model is that it illustrates the adaptive significance of "semi-speciation" and hence confirms these conclusions, including those of homeostasis (Figure 6.9). A contribution is also made to the "charr problem" since it is shown that there are adaptive reasons for why inherent sympatric speciation should be arrested.

7.7 Summary of Conclusions

The thesis examined the results of an ecosystem survey of four unexploited populations of Arctic charr at 81 °N on Ellesmere Island, Northwest Territories, Canada. Three of the lakes exhibited bimodal populations of Arctic charr and each mode was associated with different habitats and reproductive strategies. The combined conclusions of fieldwork and theory are that:-

- Alternative life history strategies should be expected to be optimised at different growth rates. This is because alternative life history strategies represent different solutions to the constraints and trade-offs imposed by energy limitation and, within a size-structured population, these will be optimised at different growth rates. These differences should be apparent both within and between different systems. (Chapter 4, Question 1).

- Dwarfs and Normals are potentially equally fit in a stable environment. In a variable environment, the fittest individual is one equipped with a "weighted coin" which allows adoption of either strategy dependent on conditions. (Chapter 4, Question 2).

- Juvenile growth rate is likely to be a good predictive stimulus on which to base the "weighted coin". Thorpe *et al.* (1989) experimentally demonstrated that smolting

in Atlantic salmon was a function of growth rate. The optimal "weighted coin" for selection of a Normal life history strategy was predicted to be of a similar form.

- A high proportion of Normal charr in any given system is likely to be associated with high average juvenile growth rates. (Chapter 4, Question 3).

- Maximum individual fitness is probably achieved in a "semi-speciated" configuration. Assuming that a common gene pool limits adaptation to any one habitat, this achieves a compromise between the rapid response to perturbation maintained by a single species stock; and the fitness advantages which may accrue as a result of specialist adaptations in steady state conditions. This state is probably maintained by assortative mating. (Chapter 4, Question 4).

- Cannibalism may contribute to the maintenance of bimodal population structures. Evidence for this is accumulated from theoretical prediction, morphological adaptations by Normal charr, direct but infrequent observation of cannibalism and parasite data.

Appendix A PASCAL Program for Optimisation of Dwarf Strategy

(Chapter 5)

```
{Program to calculate the optimum von Bertalanffy parameters for the Dwarf Strategy}

PROGRAM vonbrep;

VAR

F              : Real;   {Calculated Fitness}
Fmaxt,Fmaxk    : Real;   {Running maximum fitnesses}
w0,w           : Real;   {Initial weight, weight}
u,mu,S         : Real;   {Dummy, inst. mortality rate, Survivors}
t              : Real;   {Time at reproduction}
k1,k2          : Real;   {von Bertallanffy parameters}
c1,c2,c3       : Real;   {intermediate parameters to speed von B calcs}

PROCEDURE inputparameters;
BEGIN
   writeln('Inputvalues values of k1 and w0');
   readln(k1,w0);
END;


FUNCTION vonbert(A:Real):Real;  {Calculates size assuming vonB growth}
BEGIN
   vonbert:=c1*exp(3*ln(1-c2*exp(-1*c3*A)));

END;

                                        { MAIN PROGRAM }

BEGIN

   inputparameters;                              { Habitat parameters }
   k2:=2*k1;
   Fmaxk:=0;
```

```
{Outer loop compares the maximum fitness achieved for each value of k2 until a
maximum is calculated}

   REPEAT
   BEGIN
      t:=0;
      S:=1;
      Fmaxt:=0;

      k2:=k2+0.1;
      c1:=exp(3*ln(k2/k1));
      c2:=(1-(k1/k2*exp(ln(w0)/3)));
      c3:=k1/3;

{Inner loop calculates the fitness of an individual of a given k2 assuming spawning at
time,t.  The maximum value achieved represents the fitness at an optimised age at
reproduction}

         REPEAT
         BEGIN
            t:=t+0.1;
            w:=vonbert(t);
            u:=k2*exp(-1/3*ln(w))-k1;
            mu:=0.1+exp(2*ln(Abs(u)))/5;
            S:=S*exp(mu * -0.1);
            F:=exp(1.2*ln(w)) * S;
            IF F>Fmaxt THEN Fmaxt:=F;   {Fmaxt is the maximum fitness achieved
                                         by an individual of given k2 if timing
                                         of reproduction is optimised}
         END
         UNTIL F<Fmaxt;
         IF Fmaxt>Fmaxk THEN Fmaxk:=Fmaxt;
         END
         UNTIL Fmaxt<Fmaxk;             {Fmaxk is the maximum fitness over all
                                         possible k2's}


Writeln(' Optimal Value of k2 is ',k2-0.1);
Writeln(' Which occurs at Age', t-0.1,' Size ',vonbert(t-0.1),' and Fitness ',Fmaxk);

END.
```

Appendix B PASCAL Program for Optimisation of Normal strategy

(Chapter 5)

```
{Program to calculate the optimum von Bertalannfy parameters for the Normal
Strategy}


PROGRAM vonbrec;

VAR

w0,w,Wth      : Real;  {Initial size, weight, size at  recruitment}
u,mu,S,Smax   : Real;  {Dummy, inst. mortality rate, Survivors}
t             : Real;  {Time}
k1,k2         : Real;  {von Bertallanffy parameters}
c1,c2,c3      : Real;  {Intermediate parameters to speed von Bertallanffy
                        calculations}

PROCEDURE inputparameters;
BEGIN
        writeln('Inputvalues values of k1,w0 and Wth');
        readln(k1,w0,Wth);
END;



FUNCTION vonbert(A:Real):Real;
BEGIN
        vonbert:=c1*exp(3*ln(1-c2*exp(-1*c3*A)));
END;

                                { MAIN PROGRAM }

BEGIN

        inputparameters;              { Habitat parameters }
        k2:=k1 * exp(1/3*ln(Wth))+0.01;
        Smax:=0;
```

```
REPEAT
BEGIN
        t:=0;
        S:=1;

        k2:=k2+0.01;
        c1:=exp(3*ln(k2/k1));
        c2:=(1-(k1/k2*exp(ln(w0)/3)));
        c3:=k1/3;
```

{Loop calculates the number of survivors to reach Wth for each value of k2 and finds the maximum}

```
                REPEAT
                BEGIN
                        t:=t+0.1;
                        w:=vonbert(t);
                        u:=k2*exp(-1/3*ln(w))-k1;
                        mu:=0.1+exp(2*ln(Abs(u)))/5;
                        S:=S*exp(mu * -0.1);
                END
                UNTIL w>Wth;
                IF S>Smax THEN Smax:=S;
                END
                        UNTIL S<Smax;
        Writeln(' Optimal Value of k2 is',k2-0.01);
        Writeln(' Maximum Survival is ',Smax);
END.
```

Appendix C Choice of Default Parameters

(Chapter 6)

This appendix is intended to provide Chapter 6 with parameters which reflect the individual optimisations of fitness which occur within each habitat. It also expands upon the connection between field data, fitness and unstructured and stage-structured population models. It should be apparent that the calculations of individual optimisations of fitness could be calculated using whatever measure of fitness is most appropriate to the system under study. The main body of the paper requires these optimised parameters as input to the models, but is insensitive as to how they were calculated.

C.1 Typical Field data values

The following rough values are taken from unpublished data for Lake C, Borup Fjord 81 °N (Parker & Johnson 1991).

A Dwarf spawns at Age 8 and weight 40 g

Recruitment from Dwarf to Normal occurs at Age 8.

A Normal spawns at Age 16 and weight 160 g.

Energy invested in reproduction is approximately proportional to weight.

C.2 Mortality Values

Assuming that the individual has achieved an optimal age and size at maturity, the time to maturity (8 years for both strategies) is related to mortality rate. A very crude calculation of fitness optimisation under a constant mortality regime, μ, assumes linear growth rates, semelparity and energy invested in reproduction proportional to body size. Fitness is assumed to be measured in terms of the energy transfer of somatic tissue to reproductive tissue per unit time:-

The expected Fitness for an individual spawning at time, T, is proportional to size x P(survival)

$$= \quad T \,.\, \exp(-\mu.T)$$

This will be maximised with respect to age at maturity by $d(Fitness)/dT = 0$.

$$\text{ie} \quad T.\mu.\, \exp(-\mu.T) - \exp(-\mu.T) = 0$$

$$=> \quad \mu = 1/T$$

Given Time to Maturity, T, is 8 years for both strategies, this gives $\mu = 1/8 = 0.125$.

C.3 Fecundity Values

The ratio of Dwarf to Normal fecundity is 1:4 (Field data). For the stage-structured models, fecundities of $r_d = 10$ and $r_n = 40$ were used. This gave similar equilibrium values for both separate and single stock models.

For the unstructured models, the fecundities were scaled relative to the delayed models to ensure that similar equilibrium values were achieved. Given μ_d as found in section B. D^* as an output from the stage-structured model, and K_d this gives a value of r_d which is close to 1.5, whilst $r_n = 6$ preserves the ratio observed in the field. The biological interpretation of this scaling is that, during the time prior to maturity, each individual is subject to a mortality risk as an immature. Immatures are not modelled in the unstructured model and this scaling constitutes an approximation to the cumulative mortality risk during that stage.

Appendix D SOLVER Templates for Competition model

(Model C, Chapter 6)

```
{*************************************************************************}
{**                                                                     **}
{****  gesscomp.CON -bimodal/2 resource population -                  ****}
{**            Strategies in competition                                **}
{**            optimal switch                                           **}
{**            Environment, Kd, Kn, G can be driven                     **}
{**                                                                     **}
{*************************************************************************}

CONST  NoofStaVar   = 9; {1;  Ds - Numbers of specialist Dwarfs
                          2;  Js - Numbers of specialist juv. Normals
                          3;  Ns - Numbers of specialist Normals
                          4;  Dg - Numbers of generalist Dwarfs
                          5;  Jg - Numbers of generalist juv. Normals
                          6;  Ng - Numbers of generalist Normals
                          7;  bigG - Recruitment Factor
                          8;  Kd - Carrying capacity of Dwarf habitat
                          9;  Kn - Carrying capacity of Normal habitat}

       NoofHisVar   = 1;

       NoofOptVar   = 4;
       NoofPltVar   = 5;

       NoofCoeffs   = 7;     {1;  Gbar - longterm av. recruitment term
                              2;  Gamp - Amplitude of G variation
                              3;  Kdbar - longterm av. carrying capacity
                              4;  Kdamp - amplitude of Kd oscillation
                              5;  Knbar - longterm av. carrying capacity
                              6;  Knamp - amplitude of Kn oscillation
                              7;  T - period of oscillation}

       RingBufLen   = 0;

       NoofSwitches = 1;
```

```
{************************  MODEL PARAMETERS  ***********************}

rds = 1.5;   {intrinsic rate of increase of dwarfs}
rns = 6.0;   {intrinsic rate of increase of Normals}
rdg = 1.5;   {intrinsic rate of increase of dwarfs}
rng = 6.0;   {intrinsic rate of increase of Normals}

muds = 0.125;  {death rate of spec. dwarfs in Dwarf Habitat}
mujs = 0.125;  {death rate of spec. norms. in Dwarf Habitat}
muns = 0.125;  {death rate of spec. norms. in normal habitat}
mudg = 0.125;  {death rate of gen. dwarfs in Dwarf Habitat}
mujg = 0.125;  {death rate of gen. juv. norms. in Dwarf Habitat}
mung = 0.125;  {death rate of gen. norms. in normal habitat}

Do = 0.01;   {recruitment limiting term}
```

```
{**********************************************************************}
{**                                                                  **}
{****   gesscomp.def -bimodal/2 resource population                ****}
{**             Strategies in competition                            **}
{**             optimal switch                                       **}
{**             Environment, Kd, Kn, G can be driven                 **}
{**                                                                  **}
{**********************************************************************}

{These global variables required for the rational function interpolation of pofn vs. G.
see Figure 6.7}

CONST
  np = 5;
TYPE
  RealArrayNP = ARRAY [1..np] OF real;

{Procedure ratint is a 'bolt-on' module from 'Numerical recipes'}

PROCEDURE ratint(VAR xa,ya: RealArrayNP;
                     n: integer;
                     x: real;
                 VAR y,dy: real);
label 99;
CONST
  tiny = 1.0e-25;
VAR
  ns,m,i: integer;
  w,t,hh,h,dd: real;
  c,d: ^RealArrayNP;
BEGIN
  new(c);
  new(d);
  ns := 1;
  hh := abs(x-xa[1]);
  FOR i := 1 TO n DO BEGIN
    h := abs(x-xa[i]);
    IF h = 0.0 THEN BEGIN
      y := ya[i];
      dy := 0.0;
      goto 99
    END
    ELSE IF h < hh THEN BEGIN
      ns := i;
      hh := h
    END;
    c^[i] := ya[i];
```

```
    d^[i] := ya[i]+tiny
  END;
  y := ya[ns];
  ns := ns-1;
  FOR m := 1 TO n-1 DO BEGIN
    FOR i := 1 TO n-m DO BEGIN
      w := c^[i+1]-d^[i];
      h := xa[i+m]-x;
      t := (xa[i]-x)*d^[i]/h;
      dd := t-c^[i+1];
      IF dd = 0.0 THEN BEGIN
        writeln('pause in routine RATINT');
        readln
      END;
      dd := w/dd;
      d^[i] := c^[i+1]*dd;
      c^[i] := t*dd
    END;
    IF 2*ns < n-m THEN dy := c^[ns+1]
    ELSE BEGIN
      dy := d^[ns];
      ns := ns-1
    END;
    y := y+dy
  END;
99:
  dispose(d);
  dispose(c)
END;
```

{Procedure calcpn finds the ESS value of pofn from an input of G. It accurately calculates the function shown in Figure 6.7. It is included as a procedure rather than in the main program to avoid messy code and extra variables in the main program}

```
PROCEDURE calcpn(VAR bigG,pofn:DOUBLE);
VAR xa:RealArrayNP;  ya:RealArrayNP;
   n:INTEGER;       x, y, dy:DOUBLE;

BEGIN

{Input known values of pofn vs. G}

  xa[1]:= 1.03749;   ya[1]:= 0.002631;
  xa[2]:= 1.26846;   ya[2]:= 0.301593;
  xa[3]:= 1.56487;   ya[3]:= 0.569636;
  xa[4]:= 1.93055;   ya[4]:= 0.801451;
  xa[5]:= 2.35798;   ya[5]:= 0.99486;
```

```
  n:=np;
  x:=bigG;

  ratint(xa,ya,n,x,y,dy);

{Limit pofn to 0<pofn<1}

  IF y>1 THEN y:=1;
  IF y<0 THEN y:=0;
  pofn:= y;

END;

PROCEDURE Get_History( VAR H:HVEC; C:CVEC; t:DOUBLE );

BEGIN
END;

PROCEDURE Get_Initial_State( VAR I:SVEC; C:CVEC );
VAR Gbar, Kdbar, Knbar:DOUBLE;

BEGIN
  Gbar:=C[1];  Kdbar:=C[3];  Knbar:= C[5];

  I[7]:= Gbar;
  I[8]:= Kdbar;
  I[9]:= Knbar;

END;

PROCEDURE Get_Gradient( VAR G:SVEC; S:SVEC; C:CVEC; t:DOUBLE );
CONST pi = 3.141592654;
VAR  Ds, Js, Ns, Dg, Jg, Ng, bigG, Kd, Kn:DOUBLE;
    Gbar, Gamp, Kdbar, Kdamp, Knbar, Knamp, T:DOUBLE;
    tot1, tot2, recruits, recruitg, pofn:DOUBLE;

BEGIN

  Ds:=S[1]; Js:=S[2]; Ns:=S[3]; Dg:=S[4]; Jg:=S[5]; Ng:=S[6]; bigG:=S[7];
       Kd:=S[8]; Kn:=S[9];
  Gbar:=C[1]; Gamp:=C[2]; Kdbar:=C[3]; Kdamp:=C[4]; Knbar:=C[5];
       Knamp:=C[6]; T:=C[7];

{Total individuals in each habitat}

  tot1:= Ds + Js + Dg + Jg;
  tot2:= Ns + Ng;
```

```
{Find value of pofn as bigG varies}

  calcpn(bigG,pofn);

{Oscillation in Dwarf Carrying Capacity, Kd, Recruitment factor}

  G[7]:= Gamp * 2 * pi/T * cos(2*pi/T * t);
  G[8]:= Kdamp * 2 * pi/T * cos(2*pi/T * t);
  G[9]:= Knamp * 2 * pi/T * cos(2*pi/T * t);

{Population dynamics}

  recruits:= bigG * Js/(tot1 + Do) * exp(-tot2/Kn);
  recruitg:= bigG * Jg/(tot1 + Do) * exp(-tot2/Kn);

  G[1]:= rds *Ds * exp(-tot1/Kd) - muds * Ds;
  G[2]:= rns* Ns * exp(-tot1/Kd) - mujs * Js - recruits;
  G[3]:= recruits - muns * Ns;
  G[4]:= (rdg*Dg + rng*Ng) * (1 - pofn) * exp(-tot1/Kd) - mudg * Dg;
  G[5]:= (rdg*Dg + rng*Ng) * pofn * exp(-tot1/Kd) - mujg * Jg - recruitg;
  G[6]:= recruitg - mung * Ng;

END;

PROCEDURE Get_Memo( VAR memo:MPAD; S:SVEC; C:CVEC; t:DOUBLE );
VAR  Ds, Js, Ns, Dg, Jg, Ng, bigG, Kd, Kn:DOUBLE;
     Gbar, Gamp, Kdbar, Kdamp, Knbar, Knamp, T:DOUBLE;
     tot1, tot2, recruits, recruitg, pofn:DOUBLE;

BEGIN

  Ds:=S[1]; Js:=S[2]; Ns:=S[3]; Dg:=S[4]; Jg:=S[5]; Ng:=S[6]; bigG:=S[7];
       Kd:=S[8]; Kn:=S[9];
  Gbar:=C[1]; Gamp:=C[2]; Kdbar:=C[3]; Kdamp:=C[4]; Knbar:=C[5];
       Knamp:=C[6]; T:=C[7];

{Total individuals in each habitat}

  tot1:= Ds + Js + Dg + Jg;
  tot2:= Ns + Ng;
```

```
WITH memo DO
    BEGIN
        opt[1]:= Ds;          plt[1]:= opt[1];
        opt[2]:= Ns;          plt[2]:= opt[2];
        opt[3]:= Dg;          plt[3]:= opt[3];
        opt[4]:= Ng;          plt[4]:= opt[4];
        plt[5]:= 1;

    END;

END;
```

Appendix E MATLAB Program to Analyse Dynamic Response Characteristics near Equilibrium for Single and Separate Stocks Models.

(Chapter 6)

```
% Program sor.m.  Plots positive real part of the dominant eigenvalue of
% both charr models as recruitment variable, G, is varied.

% Define 3x3 variable: A

  A=zeros(3,3);

% Define dummy variable for ordering eigenvalues

  dummy = 0 + i*1;

% Parameters of model.  (Default parameters.  Appendix C)

   % death rates
  mud=0.125;
  muj=0.125;
  mun=0.125;

   % habitat size
  Kd=10;
  Kn=10;

   % fecundities
  rd=1.5;
  rn=6;

   % recruitment limiting term
   Do=0.01;

% There are different equilibrium values for each value of G.  (see Figure 6.5).  These
% are stored in file sepstab.dat in column format [ D*, J*, N*, G] and were
% calculated using the utility CONTOUR, which is part of the SOLVER toolset.

  load sepstab.dat -ascii;
  [m,n]= size(sepstab);
```

```
%   sets up output matrices rlocfac, rlocsep

    rlocsep = zeros(m,7);
    rlocfac = zeros(m,7);
    domeig = zeros(m,3);

%   calculates linearised matrix for each value of G and stores eigenvalues in matrices
%   rlocfac and rlocsep as appropriate.  The Partial Differential equations were
%   checked using the program MATHEMATICA.

    for i = 1:m,

% reads equilibrium values from SEPSTAB.DAT  (ESS values)

    D = sepstab(i,1);
    J = sepstab(i,2);
    N = sepstab(i,3);
    G = sepstab(i,4);

%  CALCULATING EIGENVALUES FOR SINGLE STOCK MODEL

    % calculate adaptive switch values, Pn, Pd

        Pn = rn * N/(rd*D + rn*N);
    Pd = 1 - Pn;

% dummy variables  (density dependence)

    rhod = exp(-(D+J)/Kd);
    rhon = exp(-N/Kd);

% partial derivatives for Taylor expansion

    dDrecbydD = Pd * rhod * (rd -(rd*D + rn*N)/Kd);
    dDrecbydJ = - Pd * rhod * (rd*D + rn*N)/Kd;
    dDrecbydN = Pd * rn * rhod;
    dDdeabydD = mud;
    dJrecbydD = Pn * rhod * (rd -(rd*D + rn*N)/Kd);
    dJrecbydJ = - Pn * rhod * (rd*D + rn*N)/Kd;
    dJrecbydN = Pn * rn * rhod;
    dJdeabydJ = muj;
    dNrecbydD =  -G * J * rhon/((D + J + Do)^2);
    dNrecbydJ = G * (D + Do) * rhon/((D + J + Do)^2);
    dNrecbydN = -G * J * rhon/((D + J + Do) * Kn);
    dNdeabydN = mun;
```

```
% calcs. elements of linearised matrix for facultative model

   A(1,1) = dDrecbydD - dDdeabydD;
   A(1,2) = dDrecbydJ;
   A(1,3) = dDrecbydN;
   A(2,1) = dJrecbydD - dNrecbydD;
   A(2,2) = dJrecbydJ - dJdeabydJ - dNrecbydJ;
   A(2,3) = dJrecbydN - dNrecbydN;
   A(3,1) = dNrecbydD;
   A(3,2) = dNrecbydJ;
   A(3,3) = dNrecbydN - dNdeabydN;

%  calcs. eigenvalues of A

   r = eig(A);

% routine to order eigenvalues to prevent 'cross-threading' of roots

   for j = 1:2
     if real(r(1)) <  real(r(2))
       dummy = r(1);
       r(1)=r(2);
       r(2)=dummy;
     end
     if real(r(2)) < real(r(3))
       dummy = r(2);
       r(2) = r(3);
       r(3) = dummy;
     end
   end

%  stores Real part of dominant eigenvalue in outputmatrix domeig

   domeig(i,1) = real(r(1));
```

```
% CALCULATING EIGENVALUES FOR SEPARATE MODEL

  % partial derivatives for Taylor expansion

    dDrecbydD = rd * rhod * (1 - D/Kd);
    dDrecbydJ = -rd * D * rhod/Kd;
    dDdeabydD = mud;
    dJrecbydD = -rn * N * rhod/Kd;
    dJrecbydJ = -rn * N * rhod/Kd;
    dJrecbydN = rn * rhod;
    dJdeabydJ = muj;
    dNrecbydD =  -G * J * rhon/((D + J + Do)^2);
    dNrecbydJ =  G * (D + Do) * rhon/((D + J + Do)^2);
    dNrecbydN =  -G * J * rhon/((D + J + Do) * Kn);
    dNdeabydN = mun;

  % calcs. elements of linearised matrix

    A(1,1) = dDrecbydD - dDdeabydD;
    A(1,2) = dDrecbydJ;
    A(1,3) = 0;
    A(2,1) = dJrecbydD - dNrecbydD;
    A(2,2) = dJrecbydJ - dJdeabydJ - dNrecbydJ;
    A(2,3) = dJrecbydN - dNrecbydN;
    A(3,1) = dNrecbydD;
    A(3,2) = dNrecbydJ;
    A(3,3) = dNrecbydN - dNdeabydN;

% calcs. eigenvalues of A

  r = eig(A);

% routine to order eigenvalues to prevent 'cross-threading' of root locus diagram

  for j = 1:2
   if real(r(1)) <  real(r(2))
     dummy = r(1);
     r(1)=r(2);
     r(2)=dummy;
   end
   if real(r(2)) < real(r(3))
     dummy = r(2);
     r(2) = r(3);
     r(3) = dummy;
   end
  end
```

```
    %   stores real part of dominant eigenvalue in outputmatrix domeig

        domeig(i,2) = real(r(1));
        domeig(i,3) = sepstab(i,4);      %   associated value of G

    end

% save as file domeig

    save domeig.dat domeig -ascii

%  plot of negative real part of dominant eigenvalues vs. G

    plot(domeig(:,3),-domeig(:,1))
    hold on
    plot(domeig(:,3),-domeig(:,2))
    hold off
    axis([0.0 6.0 0.0 0.15])
    title('Relative speed of Response')
    xlabel('Recruitment Factor, G')
    ylabel('Speed of response, ')
```

Appendix F Stage-structured Models

(Chapter 6)

Stage-structured versions of the models are also developed. These models are biologically more realistic because they allow for development time. A formulation which is common to both separated and single stock models once the individual has been 'allocated' its life history strategy is illustrated at Figure F.1. Tables F.1 and F.2 describe the mathematical formulation, which is otherwise similar to the undelayed versions.

In general, the terms of the model are identical to the unstructured versions (Table 6.1) except where outlined in Table F.1. Three development times are included:- Time to maturity for Dwarfs, minimum time to Dwarf/Normal Recruitment and time post recruitment for a Normal to mature. A Normal pre-recruit stage is included to allow for the density-dependent transition from Juvenile Normal to Normal.

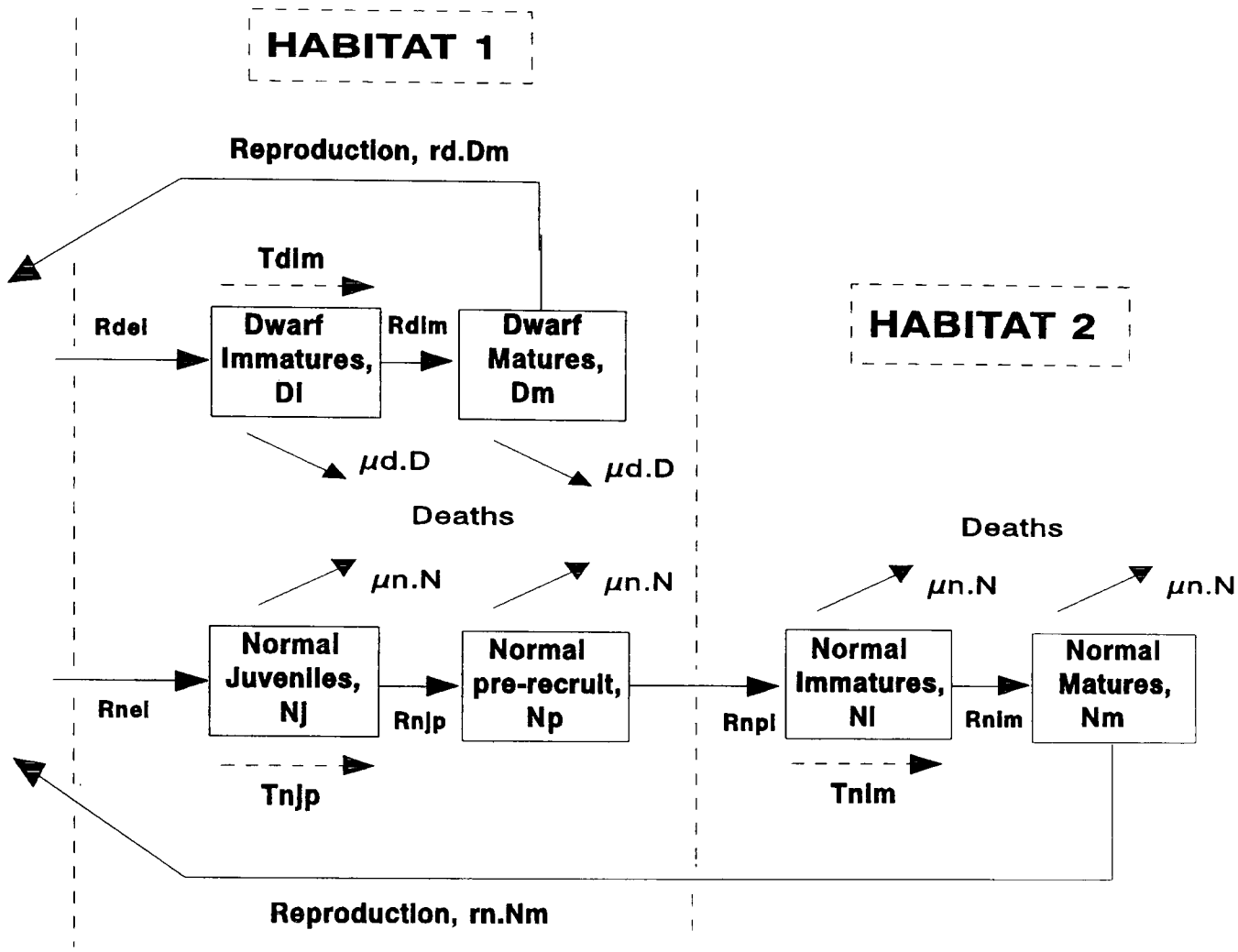


Figure F.1 Model of a bimodal population structure incorporating developmental delays (the "stage-structured" model). The same habitat, recruitment and reproductive structure is maintained as for the unstructured versions; and the two means of allocation of life history strategy are identical. The developmental delays modelled are both ages at maturity, and a minimum time to recruitment as a Normal. A "buffer" of Normal "pre-recruits", Np, exists within Habitat 1 and provides recruits to Habitat 2 when "space" becomes available.

	Symbol	Default Value	Brief Description
Variables	D_i		Immature Dwarfs
	D_m		Mature Dwarfs
	N_j		Juvenile Normals in Dwarf Habitat
	N_p		Normal pre-recruits waiting for 'space' in Normal habitat
	N_i		Immature Normals in Normal habitat
	N_m		Mature Normals
	Tot_d		$= D_i + D_m + N_j + N_p$, Occupants of Dwarf habitat
	Tot_n		$= N_i + N_m$, Occupants of Normal habitat
Parameters	T_{dim}	8 yrs	Age at Maturity for Dwarfs
	T_{njp}	8 yrs	Minimum time to Dwarf/Normal Recruitment
	T_{nim}	8 yrs	Age post recruitment for Maturity as a Normal
	G'	10	Recruitment Factor

Table F.1 Variables and parameters unique to the Stage-structured versions of the bimodal stock model. The remainder are the same as Table 6.1.

	Symbol	Separate Stocks	Single Stock
Recruitment Rates	$R_{dei}(t) =$	$r_d.D_m.\exp(-Tot_d/K_d)$	$(r_d.D_m+r_n.N_m).P_d$ $x \exp(-Tot_d/K_d)$
	$R_{nej}(t) =$	$r_n.N_m.\exp(-Tot_d/K_d)$	$(r_d.D_m+r_n.N_m).P_n$ $x \exp(-Tot_d/K_d)$
	$R_{dim}(t) =$	$R_{dei}(t-T_{dim})$.	$\exp(-\mu_{di}.T_{dim})$
	$R_{njp}(t) =$	$R_{nei}(t-T_{njp})$.	$\exp(-\mu_{nj}.T_{njp})$
	$R_{npi}(t) =$	$G.N_p/(Tot_d+D_o)$.	$\exp(-Tot_n/K_n)$
	$R_{nim}(t) =$	$R_{npi}(t-T_{nim})$.	$\exp(-\mu_{ni}.T_{nim})$
Balance Equations	$\frac{dDi}{dt} =$	$R_{dei}(t) - \mu_{di}.D_i - R_{dim}(t)$	
	$\frac{dD_m}{dt} =$	$R_{dim}(t) - \mu_{dm}.D_m$	
	$\frac{dN_j}{dt} =$	$R_{nej}(t) - \mu_{nj}.N_j - R_{njp}(t)$	
	$\frac{dN_p}{dt} =$	$R_{njp}(t) - \mu_{np}.N_p - R_{npi}(t)$	
	$\frac{dN_i}{dt} =$	$R_{npi}(t) - \mu_{ni}.N_i - R_{nim}(t)$	
	$\frac{dN_m}{dt} =$	$R_{nim}(t) - \mu_{nm}.N_m$	

Table F.2 Formulation of the continuous time differential equations used in the Stage-structured versions of the bimodal stock models

Glossary[1]

Abundance - (Parasitology). The average number of parasites per host. (Margolis *et al.* 1982).

Allopatric - Living in different geographic areas; compare with *sympatric*. (Guttman & Hopkins 1983).

Altricial - of, or pertaining to, late maturity.

Anadromous - A sea-migrating salmonid.

Assortative mating - Mating with a like individual.

Dispersion - (Parasitology). Description of the overall form of a statistical distribution. (Anderson & Gordon 1982).

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[1] This glossary includes subject-specific terminology to assist the non-specialist. The subject is indicated in brackets after the definition, where appropriate.

Evolutionarily Stable Strategy (ESS) - A strategy such that, if most members of the population adopt it, there is no mutant strategy that would give higher reproductive fitness. (Maynard Smith & Price 1973).

Facultative - Having different modes of activity, depending on conditions. (Guttman & Hopkins 1983).

Fitness - The expected contribution of an allele, genotype, or phenotype to future generations. The fitness of genes and organisms is always relative to the other genes and organisms that are present in the population. It is also a function of the environment in which it is measured. (Stearns 1992)

Genotype - A description of the particular set of genes an organism carries, as contrasted by its appearance (see *phenotype*). (Guttman & Hopkins 1983).

Gonadosomatic index (GSI) - The weight of the gonad relative to the total weight of the fish expressed as a percentage.

Heterochrony - *Phyletic* change in the onset or timing of development, so that the appearance or rate of development of a feature in a descendant *ontogeny* is

either accelerated or retarded relative to the appearance or rate of development of that feature in an ancestor's *ontogeny*. (de Beer 1958).

Homeostasis - (Population structure). The stable condition that a population tends to maintain through compensatory adjustments to changing conditions. Note that this term is usually used with reference to organisms rather than populations. (*sensu* Guttman & Hopkins 1983).

Iceout - When a lake achieves 100% open water for the first time.

Infrapopulation - (Parasitology). The population of parasites within a given host. (Margolis *et al.* 1982).

Intensity - (Parasitology). Number of individuals of a parasite species in each infected host. (Margolis *et al.* 1982).

Life History Strategy - The broad features of a life cycle. A successful life history strategy optimises trade-offs between growth, reproduction and mortality.

Littoral - Growing or living near the shore.

Mode - A size class of Arctic charr.

Morph - Used interchangeably with the term *mode*. Often morphological (shape) differences are associated with different size modes, hence the use of *morph*.

Ontogeny - The life history of an individual, both embryonic and post-natal. (Gould 1977).

Otolith - plate-like bone found in the vestibule of the ear and part of the system of balance. The age of the fish can be determined by counting growth rings in the otolith in a similar manner to a tree.

Paedomorphosis - The retention of ancestral juvenile characters by later *ontogenetic* stages of descendants. (Gould 1977).

Parr - A juvenile freshwater-resident stage of the salmonid life cycle.

Phenotype - A description of the appearance (or other manifestation) of an organism, as contrasted with its *genotype* (q.v.). (Guttman & Hopkins 1983).

Phylogeny - The evolutionary history of a lineage, conventionally (though not ideally) depicted as a sequence of successive adult stages. (Gould 1977).

Piscivorous - fish-eating.

Planktonivorous - Plankton-eating.

Precocial - Of, or pertaining to, early maturity

Prevalence - (Parasitology). Number of individuals of the host species infected with a particular parasite divided by the number of hosts examined. (Margolis *et al.* 1982).

Profundal - inhabiting the zone of deep water and bottom.

Reaction Norm - The full set of phenotypes that a genotype will express in its interaction with the full range of environments in which it can survive. (Stearns 1992)

Smolt - A juvenile stage of the salmonid life cycle normally associated with first seaward migration.

Soma - Any part of the organism other than gametes and their precursors. (Guttman & Hopkins 1983).

Stage-structure - (Modelling). A stage-structured model incorporates time delays, whereas an unstructured one does not.

Stunted population - A unimodal population consisting of stunted Dwarf individuals.

Sympatric - Living in the same geographical region; compare with *allopatric*. (Guttman & Hopkins 1983).

Ultraoligotrophic - Description of a system with very low nutrient levels.

"Weighted Coin" A *facultative reaction norm* which determines choice of *life history strategy*.

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BF/PD/35

GEOGRAPHISCHES INSTITUT
UNIVERSITÄT HEIDELBERG
Prof. Dr. Dietrich Barsch

6900 HEIDELBERG 1
Im Neuenheimer Feld 348
Postfach 105760
Telefon 564570

13.6.1989

Geographisches Institut der Universität Heidelberg
Im Neuenheimer Feld 348, 6900 Heidelberg 1

Lieutenant H.H. Parker BA
Royal Navy
Makrhuset
Gamles Lane
Woodmancote - GL52 4PU
CHELTENHAM / Englang

ba/oe

Dear Mr. Parker:

It was very interesting to hear from your research at the lakes in Midnight Sun Valley. Unfortunately you did not meet some of my former students like Lorenz King, now professor at the University of Gießen, who camped 1988 for two weeks at the snout of Carl Troll glacier.

Your question regarding the time of landlocking of your trout ("Forelle") it is not easy to decide. Let me put it this way:

(1) We think that Midnight Sun Valley was already free of glacier ice some 35.000 years ago (cf. Barsch, King & Mäusbacher 1981).

(2) The broad valley floor of Midnight Sun Valley was probably built up 15.000 to 17.000 years ago. Later it was isostaticly lifted at its present altitude some 80 m above sealevel.

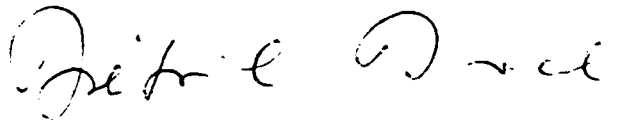
(3) But the crucial problem is the age of the lakes itself. They seem to belong to a glacial advence which is tentatively put by King (1981) around 20.000 years B.P.

Taking all together, the lakes on the valley floor (like Access lake) are probably not older than 15 to 20.000 years, they are surely not younger than 6.000 years. Hopefully, this will help you.

/2

By the way, is it really necessary that the trout had to swim into the lake? Often fishes (that is: their eggs) are transported in the feathers of waterfowls (like ducks); and there are ducks nesting in that area during summer.

With my very best regards.
Yours sincerely,



(Prof. Dr. Dietrich Barsch)

University of Exeter

DEPARTMENT OF BIOLOGICAL SCIENCES

Hatherly Laboratories, Prince of Wales Road, Exeter EX4 4PS

Telex: 42894 EXUNIV G
Switchboard: 0392 - 263263

Professor John A Bryant
Head of Department
0392 - 264672

Professor Clive R Kennedy
0392 - 263757

Professor David Nichols
0392 - 263789

Professor John Webster
0392 - 263784

2 June 1989

Dear Henry,

Please find enclosed the short report on the parasites that I promised you, and accept my apologies for its being a few days late.

It may be rather too long for your purposes. If so, please feel free to shorten it as you see fit. Even with your guidelines I was not quite sure exactly what you wanted, or in what format. As you will not doubt be completing your own section on charr, you can adapt this as you see fit. Please do not hesitate to make wording less scientific, or to come back to me for clarification if necessary.

You will see that I have only analysed by lake and not by morph. The reason for this is in part brevity, but also the small sample sizes of the larger morph in lakes B and C. In the main lake you will see I had to restrict the sample size to 50, that being the number of fish for which I could obtain detailed quantitative estimates of Diphyllobothrium. I could try to split by morphs if you wished, but I doubt its value as sample sizes have to be good to produce any statistically valid distinctions.

I hope this is what you wanted, and that you are close to finishing your sections. I am doing some preliminary work on preparing a more general paper along the lines we discussed, but this may take some time.

Very best wishes,
Yours sincerely,

C.R.Kennedy

Parasitic infections of the charr

Introduction

Although parasites of charr have been studied in many localities on the mainland of America, Asia and Europe, they have been studied in far fewer localities on Arctic islands. Extensive investigations have been undertaken on Novaya Zemlya and on Bear Island in Europe, and the results tend to show that the parasite fauna of charr on these islands is similar to that on the mainland, and may or may not be as rich and diverse. In association with the studies on charr themselves, therefore, the opportunity was taken to examine their parasites, with the specific aims of determining whether the parasites of charr on high Arctic islands in Canada were similar to those of mainland charr, similar to those of charr on high Arctic European islands and more or less rich than on the mainland.

Methods

Charr were examined by standard techniques, and all major organs were examined for the presence of metazoan parasites. Protozoa were not searched for, nor was the blood system examined. The numbers of individuals of each parasite species was recorded for fish in Lakes A,B and C. Some fish in the main lake were very heavily infected and precise numbers of their parasites were not determined in all cases. The results in the table therefore refer only to the subsample of fish for which all parasite numbers were recorded. All identifications were confirmed on material brought back to England.

Results

Four species of parasites were found altogether. The copepod Salmincola edwardsii occurs on the gills and inner operculum : the tapeworm Diphyllobothrium dendriticum occurs as the larval stage, encysted on the stomach and other organs in the body cavity : the adult tapeworms Proteocephalus sp. and Eubothrium salvelini occur in the intestine. Identification of Diphyllobothrium follows current opinion, but identification of proteocephalid tapeworms is both difficult and uncertain. The material was probably P.tumidocollus .

Infection levels differed considerably from lake to lake (Table). Two species were found in all four lakes (D.dendriticum and Proteocephalus), and only these two in the highest lake (A). Lake B contained in addition E.salvelini. The prevalence and intensity of each species also varied from lake to lake. S.edwardsii was most abundant and prevalent in the main lake. D.ditremum was least common in Lake B, was more common in Lake C and dominated Lake A, but reached its maximum abundance in the Main Lake where one fish harboured just over 4000 individuals. Levels of Proteocephalus were comparable in Lakes A,B and C but this species was very rare in the Main Lake, where by contrast E.salvelini was the commonest and most abundant intestinal tapeworm. With the exception of Proteocephalus, therefore, all species were most prevalent and abundant in the main lake.

Table

Parasitic infections of the charr

	Lake A	Lake B	Lake C	Main Lake
No. of fish examined	32	26	57	60
% of fish infected	81.2	65.4	57.9	86.7
Salmincola edwardsii				
Prevalence	0	0	5.3	18.3
Mean (Max.) intensity	0	0	1 (1)	11.7 (51)
Diphyllobothrium ditremum				
Prevalence	75.0	21.1	24.6	75.0
Mean (Max.) intensity	13.6 (75)	1.7 (3)	10.1 (84)	300.0 (4242)
Proteocephalus sp.				
Prevalence	53.0	42.3	33.3	1.7
Mean (Max.) intensity	9.0 (48)	9.5 (32)	10.6 (48)	1.0 (1)
Eubothrium salvelini				
Prevalence	0	34.7	12.3	43.3
Mean (Max.) intensity	0	1.3 (2)	1.6 (3)	3.4 (20)

Prevalence = % of fish infected : Intensity = no. of parasites per infected fish.

Discussion

All four species of parasite have been recorded from charr in other locations in Canada, and they, or their European equivalent, from charr in Europe. The general characteristics of the parasite fauna of charr on Ellesmere Island are fairly similar to those on Bear Island in the Norwegian Arctic. There an additional species of nematode was present, but otherwise the same four species and with all four increasing in abundance in the largest lake. On Bear Island also the fauna tended to be dominated by D. ditremum. The variations in prevalence and abundance between the lakes may reflect differences in size and altitude of the lakes, or, probably related, differences in the composition of the zooplankton which serve as intermediate hosts for all three species of tapeworm or differences in the proportions of the different types or morphs of charr in each lake.

It can thus be concluded that the parasites of charr on Ellesmere Island are indeed similar to those on the mainland. Most lakes on the mainland have a slightly richer parasite fauna, as species of flukes and nematodes may also be present. The restriction of the parasite fauna to those species having a planktonic larval stage or utilising planktonic intermediate hosts was also characteristic of the parasite fauna of charr on Bear Island, and indeed one of the most interesting conclusions of the survey was to see how similar was the parasite fauna of charr on high Arctic Islands in Canada and Europe. It is hoped that this similarity will form the theme of a publication elsewhere.

C. Kennedy

BF/PD/33

UNIVERSITETET I BERGEN
ZOOLOGISK MUSEUM
Muséplass 3, 5007 Bergen
Tlf. (05) 21 29 05
Systematisk avd. (05) 21 29 04
Økologisk avd. (05) 21 22 24

UNIVERSITY OF BERGEN
MUSEUM OF ZOOLOGY
Muséplass 3, N-5007 Bergen,
Norway
Phone: +47 5 21 30 50

BERGEN, April 28, 1989

J. nr.

Lieutenant H. H. Parker, BA Royal Navy
Markhuset
Gambles Lane
Woodmancote
Celtenham
GL52 4PU
England.

Dear Lt. Parker

Thank you for your letter and the samples sent to prof. Sæther. He asked if I would identify the species, and with a little help from other people at the Museum (on groups other than chironomids) I have worked out the enclosed list of identifications. Prof. Sæther have confirmed some of the identifications.

The new species of Heterotrissocladius is possibly a predator on the larvae of the caddis fly Apatania zonella. A larval exuviae of an undescribed type of Heterotrissocladius was found inside the caddis fly house. The new genus near Stictochironomus could conceivably also be an undescribed type of that genus. It keys near Stictochironomus, but differs in several important details. I would be very interested in receiving additional material of this species, most of all larvae. These will be rather large (between 15 and 20 mm when fully grown), and red (at least when alive).

The name of the lake do not appear from the interim report. Does it have a name at all? We would like to know the name for our labels.

You will find further information on the invertebrate fauna of Ellesmere Island in: Oliver, D.R. 1963. Entomological studies in the Lake Hazen area, Ellesmere Island, including lists of species of Arachnida, Collembola, and Insecta. - Arctic 16(3):175-180. and perhaps in other publications by Oliver.

Yours sincerely

Øyvind A. Schnell

LIST OF TAXA IDENTIFIED:

Some of the samples were ruined because the lid on the vials had fallen off. The following samples were in good condition and were identified:

Sample no. 1: On lable: "Sputniks" from 022 (31/5/1).
Content: Acari indet. (Water mites).

Sample no. 2: On lable: Last year's ovary? 228 (20/8/3).
Content: Eggs of arctic charr.

Sample no. 3: On lable: Caddis larvae + case from 019 (30/5/1).
Content: Larva & case of Apatania zonella Zetterstedt.

Sample no. 4: On lable: Stomach content of 209 (20/8/1).
Content: Approx. 100 chironomid pupae of several species; the species Paracladius alpicola (Zetterstedt), Heterotrissoclaidus n. sp. and Paratanytarsus natvigi (Goetghebuer) dominated. In addition there were at least four other chironomid species.

Sample no. 5: On lable: Asst'd chironomids from fish 052-057 (20/7/1).
Content: Chironomid pupae and larvae.

New genus near Stictochironomus	4 males,	3 females.
Micropsectra sp.		4 females.
Heterotrissocladius subpilosus (Kieffer)		1 female.
Orth. larvae		3 larvae.

Sample no. 6: On lable: Stom. cont. C(?) 3 (13/8/2).
Content: Remains of chironomid larvae and zooplankton (Cladocera), not possible to identify.

Sample no. 7: On lable: Asst'd unident. flies from 083 (23/7/5).
Content:

Apamea maillardi exulis (Lef.)	1 female.	
Lymantridae groenlandicus Woc.	1 female,	1 male.
Olethreuthes inquietana (Walk.)	2 males.	

These three species belong to Lepidoptera.

Empididae sp.	1 female.	
Ichneumonidae sp.	1 female,	1 male.
Muscidae sp.	1 female.	

These insects are of terrestrial origin.

3, St. Felix Road,
Ramsey Forty Foot,
HUNTINGDON,
Cambridgeshire,
England PE17 1YH.

24.ix.91.

Dear Kate,

As predicted I have been able to start on your specimens and so far have processed two samples as far as is possible. The lists are appended.

First I must say just how well the specimens are preserved; you obviously got it just right: they are very easy to manipulate (the Russian specimens I was dealing with before fragmented at a touch).

Second, the experience is personally very exciting. For instance, the first specimen I saw in the sample from Lake A was a Zalutschia new to me (there is only one British species and the remaining European species are mainly far northern). It seemed to run to trigonacies in Ole Saether's key and two drowned adult males clinched the identification. This is a species first recorded from Ellesmere Island and still known only from the North West Territories of Canada. The liklihood that my collection would have specimens of such a species without your input is minimal. In fact, I must have the longest series of pupal exuviae of this species in any collection in the world now!

It was nice to recognize one species - Corynoneura arctica - without recourse to the literature, for it also occurs in Scotland, but all the other species are new to me.

The Sergentia will have to await my finding adult males for identification; so far only a female has turned up, but the second part of that collection from Lake H could supply when I locate it. The Chaetocladius is represented by only one exuviae so far, but I'm hopeful of associated adult material somewhere. The situation with Limnophyes is different in that there is more than one species represented as adults and pharate adults (curiously exuviae are rare in these two samples), so identification will be possible soon, but to my embarrassment I have mislaid the paper revising this genus.

In this Lake H sample there are many exuviae of a Psectrocladius which are somewhat novel in their structure and a number of adult males that I cannot place. The two contenders, i.e. the two species I don't know that are recorded for the North West Territories, are polaris and barbatimanus. The pupae of neither are described and the adult males in the sample don't match the description of polaris very well. I shall ask Don Oliver (Canadian National Collection, Ottawa) if I can borrow a reference specimen of barbatimanus as the species is very inadequately described. The situation is compounded by the presence of one exuviae of another species of Psectrocladius in the same sample, which resembles the European octomaculatus, which has to date not been recorded for the Nearctic, but it is a far northern species in Europe, so could be circumpolar in distribution. I have published papers on this genus and I sense something interesting here....

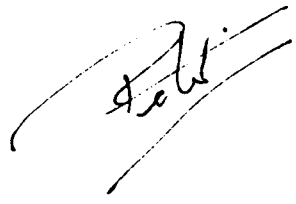
The Paratanytarsus is abundant in the Lake H sample. Only one species recorded for NWT is unknown to me so it could be that. There are adults as

well, but I haven't a description of the species and must acquire it through one of the libraries before I can put a specific name to it.

Stictochironomus devinctus has not been previously recorded north of Saskatchewan and its pupa has not to my knowledge been described....but I risk boring you, so will stop, hoping that some of the excitement I have experienced so far I have managed to convey.

Already 250 specimens have been added to my collection from these two samples - it does look as if most of the recorded species of the NWT will be represented in your material and in sufficient quantity to produce more than an adequate reference series - I cannot be more grateful for your having obtained them for me.

With every best wish,



3, St. Felix Road,
Ramsey Forty Foot,
HUNTINGDON,
Cambridgeshire,
England PE17 1YH.

11.1.91.

Dear Kate,

At last some more has been done! This time I've managed to include a sample from fish guts. On the whole the fish seem to be going for the larger pupae; all except for Procladius are about to eclose, but in the case of Procladius most of the specimens are just moulted from their larval skins. This underlines a difference in their behaviour: in the subfamily Tanypodinae, to which Procladius belongs, the pupae may spend much of their time at the water surface in the manner of mosquito pupae, whereas in the other subfamilies the pupae are hidden in silken tubes until ready to eclose.

The identification problems thrown up by the Ellesmere specimens continue to demand sleuthing of the kind that I relish - it is the real fun side of the research for the Tanytarsus niger problem: last July I collected a long series of this species in the lake at the St. Bernard Pass between Switzerland and Italy (in dense fog and a snow blizzard!) - these specimens accord precisely with the descriptions in the definitive revision of the genus. Now Ellesmere provides a series of "niger", which in both the adult and pupa differ in certain characters a little from the European specimens. Is this just an example of the other end of a range of variation, or another, closely related species? If the latter one will have to re-examine the remains of the original specimen of niger from Greenland, for it may be that the European form is the unnamed species...

This latest material I have been looking at has an adult male Micropsectra which shows my previous identification of insignilobus to be in error; it is brundini. This is quite exciting, because, if they are really distinct species (they are very close), the pupal skins you collected are the first known. Now I need a series of insignilobus exuviae for comparison....

It was very pleased to find Paracladius alpicola specimens, for with the quadrinodosus you collected as well, I now have good series of the three known species in this genus.

I hadn't realized when I reported before to you that Heterotrissocladius brundini is a new record for the Nearctic and there's no doubt as to its identity.

I have now managed to identify the Limnophyes specimens in the previous samples: interestingly, all those from Lake A are ninae, whereas the specimen from Lake H is natalensis. The three lakes continue to show marked differences - the Stictochironomus of Lake B is quite different from that of Lake H, but I haven't been able to put a name to it yet...more sleuthing!

Every best wish,

3, St. Felix Road,
Ramsey Forty Foot,
HUNTINGDON,
Cambridgeshire,
England PE17 1YH.

2.11.92.

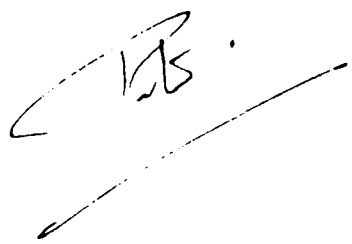
Dear Kate,

Thanks for your enthusiastic letter! I will, of course, supply you with Aims, Results and Discussion sections - for you to do with what you will - by mid-March (that man Bill is a slave-driver!!), but it must be accepted that it can only be an interim report at this stage...there must be half a million skins to look at yet (I almost daren't say that lest it suppress you in your vigour at collecting for me in Kenya! Be assured that I am committed to getting the Ellesmere material completed, but I have to keep my other projects rolling as well or there will be others disappointed and when one's research is dependent upon the goodwill of colleagues to provide the material one does try to keep everyone happy!). Correlations with air/water temperature and the like at this stage would be very tentative, but I will test out the possibility - one of the important aspects of boreal chironomid behaviour is their respective phenologies, i.e. their timing of events during the year, in particular their eclosion period: in such a short open water period there is known to be a rapid succession of species taking wing, presumably so that the limited swarming sites don't get too cluttered; already there is good evidence of this in the Ellesmere material from Lake H. Certainly there was a lot more behind your collecting of midge skins on Ellesmere than just stuffing my cabinets with interesting forms!! More will be revealed when you receive the "Interim Report".

As for my publishing elsewhere: if there are important systematic conclusions that result from the "sleuthing" to which I referred in my last letter, then I shall take on the responsibilty of getting them published, but I would hope that in the final Report all other aspects of the investigation are included. Which, because I work to deadlines, brings up the very important question: When is the last date for getting the final report submitted?

This must needs be a short communication...the microscopes are calling!...more later.

Every best wish,



Chironomidae from Ellesmere Island, leg. K. Silvester.

6.vii.91 Lake A, Midnight Sun Valley

Orthocladiinae
    Chaetocladius sp.
    Corynoneura arctica
    Cricotopus (Cricotopus) tibialis
    Limnophyes spp.
    Orthocladius (Eudactylocladius) Pe2 (Langton 1991)
    Zalutschia trigonacies
Chironominae
 Chironomini
    Sergentia sp.
 Tanytarsini
    Micropsectra insignilobus

8.vii.91 Lake H, Esayoo Bay

Orthocladiinae
    Corynoneura arctica
    Heterotrissocladius oliveri
    Limnophyes spp.
    Metriocnemus ursinus
    Psectrocladius sp1
    Psectrocladius cf. octomaculatus
Chironominae
Chironomini
    Sergentia sp.
    Stictochironomus devinctus
Tanytarsini
    Paratanytarsus sp.
    Tanytarsus gracilentus
    Tanytarsus norvegicus

Chironomidae from Ellesmere Island, leg. K. Silvester.

6.vii.91 Lake A, Midnight Sun Valley (update)

Orthocladiinae
- Chaetocladius ?perennis
- Corynoneura arctica
- Cricotopus (Cricotopus) tibialis
- Limnophyes ninae
- Orthocladius (Eudactylocladius) Pe2 (Langton 1991)
- Zalutschia trigonacies

Chironominae
Chironomini
- Sergentia sp.

Tanytarsini
- Micropsectra brundini

8.vii.91 Lake H, Esayoo Bay (update)

Orthocladiinae
- Corynoneura arctica
- Heterotrissocladius oliveri
- Limnophyes natalensis
- Metriocnemus ursinus
- Psectrocladius (Psectrocladius) sp1
- Psectrocladius (Psectrocladius) cf. octomaculatus

Chironominae
Chironomini
- Sergentia sp.
- Stictochironomus devinctus

Tanytarsini
- Paratanytarsus sp.
- Tanytarsus gracilentus
- Tanytarsus norvegicus

3.viii.91 Lake H, Esayoo Bay

Tanypodinae
- Arctopelopia cana
- Procladius ?gretis

Orthocladiinae
- Cricotopus sp.
- Heterotrissocladius brundini
- Heterotrissocladius oliveri
- Metriocnemus ursinus
- Orthocladius (Euorthocladius) roussellae
- Orthocladius (Orthocladius) charensis
- Paracladius quadrinodosus
- Parakiefferiella nigra

Chironominae
Tanytarsini
- Micropsectra brundini
- Tanytarsus cf.aberrans

18.vii.91 Lake B, Midnight Sun Valley

Tanypodinae
    Arctopelopia cana
    Procladius ?gretis
Orthocladiinae
    Corynoneura arctica
    Cricotopus (Cricotopus) pilosellus
    Cricotopus (Cricotopus) tibialis
    Cricotopus (Isocladius) laricomalis
    Heterotrissocladius brundini
    Paracladius alpicola
    Paracladius quadrinodosus
    Psectrocladius (Psectrocladius) cf.octomaculatus
    Psectrocladius (Psectrocladius) fennicus
    Zalutschia trigonacies
Chironominae
 Chironomini
    Chironomus sp.
    Sergentia sp.
    Stictochironomus sp.2
 Tanytarsini
    Micropsectra nigripila
    Paratanytarsus natvigi
    Tanytarsus cf.aberrans
    Tanytarsus near niger

18.vii.91 Lake B, Midnight Sun Valley; in fish guts

Tanypodinae
    Arctopelopia cana
    Procladius ?gretis
Orthocladiinae
    Heterotrissocladius brundini
    Psectrocladius (Psectrocladius) cf.octomaculatus
    Zalutschia trigonacies
Chironominae
 Chironomini
    Sergentia sp.
    Stictochironomus sp.2
 Tanytarsini
    Paratanytarsus natvigi
    Tanytarsus near niger

Micropsectra silvesteri n.sp.

Micropsectra cf. nigripila Langton 1992 (ecology, parthenogenesis, phenology)

Adult female (n=7, unless stated otherwise). (Only imagines positively associated with pupal exuviae are considered: 4 partly eclosed, 3 pharates. In consequence wing characters are missing from the description.)

Paler than nigripila: thorax gold with brown vittae, mesosternum and postnotum; halteres pale gold.

Antenna: Flagellum with 5 flagellomeres, flagellomere 1 with 2 whorls of setae; flagellomeres 2-4 each with 1 whorl of setae. Apical flagellomere 125-158, 141.86 µm long. Antennal ratio 0.33-0.41, 0.36.

Head: Frons without frontal tubercles. Temporal setae uniserial, 7-11, 9.71. Length of palp segments 2-5 (µm): 32-58; 100-175; 92-150; 130-225 (6). Palpal segments 3 and 4 with 20-30, 16-22 setae. Clypeals 22-32, 27.5 (6).

Thorax: Acrostichal setae 11, 12 (2). Dorsocentral setae extended forwards beyond parapsidal suture to near antepronotum, perceivable as three groups: 0-2, 1.13 near antepronotum; 1 or 2, 1.86 between anterior group and parapsidal suture; 7-14, 11.88 in uniserial posterior row. Prealars uniserial, 3 or 4, 3.86. Scutellars uniserial, 8-11, 9 (5).

Legs: Apical four fifths of mid leg tarsomere 1 with 23 (1) sensilla chaetica. Lengths (µm) and proportions of legs (n=3 unless otherwise stated):

	F	Ti	Ta1	Ta2
P1	600-1070	600-840	760 (2)	400-420 (2)
P2	710-1040	800-910	390-500	240-300
P3	1060-1300	990-1280	620-780	400-510

	Ta3	Ta4	Ta5	LR
P1	210-250 (2)	170 (2)	120-130 (2)	1.21-1.27 (2)
P2	170-230	110-140	110-120	0.49-0.55
P3	310-410	170-220	130-170	0.61-0.63

Genitalia: very similar to nigripila but dorsomesal extension of cerci more angular.

Pupa (n=20, unless stated otherwise). Total length 4.6-6.3, 5.48 mm.

Cephalothorax very pale brown, smudged with golden-brown; margins of wingsheaths and edge of suture narrowly golden-brown. Abdomen transparent; point and spinule patches gold; lateral longitudinal bands of segments VII and VIII gold; comb of segment VIII, inner half and extreme margin of anal lobes, and genital sheaths gold.

Cephalothorax: Cephalic tubercles rounded mounds with short apical nipple bearing the frontal seta. Frontal setae 135-200, 176.05 µm long. Pedicel sheath with a ridge-like flap. Margin of suture with a narrow band of small points, crowded and a little larger on the median hump. Thoracic horn elongate, 440-835, 672.8 µm long, 55-80, 62.1 µm broad; horn ratio 7.6-13, 10.34; spines on apical two thirds, diminishing in length apicad, longest spine 63-110, 87.83 µm long. 2 median antepronotal setae, 135-225, 175.53; 75-145, 95.42 µm long. 2 lateral antepronotal setae, 65-140, 103.45; 10-28, 18.4 µm long. Precorneal setae 155-210, 177.65; 75-115, 99; 100-150, 130.3 µm long. Dorsocentral setae 90-180, 126.45; 30-75, 53.23; 60-120, 94.55; 43-100, 75.2 µm long; anterior very thin and flexible, posterior robust and stiff; one anterior dorsocentral seta occasionally forked from base. Prealar mound swollen posteriorly, without projection.

Wing sheaths without nose.

Abdomen: As nigripila but lateral longitudinal bands of shagreen on tergites IV-VI less well developed, evanescing anteriorly, leaving a broad unarmed space behind the anterior transverse point patches.
Abdominal setation as in nigripila. Posterior hook row of tergite II 0.47-0.55, 0.51 (6) breadth of segment II, with 97-145, 117.08 (12) hooks. Comb of segment VIII, with 2-5, 3.26 marginal teeth, and 0-7, 2.33 (18) dorsal points. Anal lobe with fringe of 48-66, 55.75 flattened setae in a single, sometimes irregular, row. Two dorsal flattened setae on anal lobe, the anterior much thinner than the posterior.
Genital sheaths broad, triangular.

Distribution and habitat:

Known only from lakes in the Borup Fiord region of Ellesmere Island (Canadian arctic), emerging over a short period in mid-July (Langton 1992).

Reproductive behaviour

All pupal exuviae, and pharate and partly eclosed imagines are female. One pharate specimen contains discharged eggs within the pupal exuviae, a phenomenon previously noted in Paratanytarsus grimmii (Grimm 1871). It has been postulated (Langton, Cranston & Armitage 1988) that species which lay eggs close to emergence cannot be bisexual.

Taxonomic comments

Micropsectra nigripila and silvesteri are very similar, sharing characters unusual for Micropsectra: the extension of the dorsocentral seta row to the antepronotum of the adult and the elongate thoracic horn with short spines of the pupa. Also, the presence of 2 flattened dorsal setae on the anal lobes, constant in silvesteri, occasional in nigripila, has not previously been recorded for the genus. However, as silvesteri is obligately parthenogenetic, it cannot be a behavioural morph of nigripila.

Adult silvesteri is distinguished morphologically from nigripila by its paler colour (ground colour of thorax gold with obvious darker vittae and haltere knob not infuscated apically), the more or less continuous dorsocentral seta row not proliferated anteriorly and the more angular inner dorsal extension of the cerci. Pupal silvestri are unique in Micropsectra in the constant presence of two long median antepronotal setae. Other differences from nigripila include paler colour, broader thoracic horn and consequent lower horn ratio, generally shorter spines on the thoracic horn, less prominent cephalic tubercles, absence of nose on wingsheaths, reduced armament of tergites IV-VI, and generally 3 marginal teeth on gold comb of segment VIII.

Etymology

The species is named after Dr. Kate Silvester, medical officer of Expedition Ellesmere 1991, in gratitude for the very extensive collection of Chironomidae made in addition to her official duties.

Material examined:
Holotype: Partly eclosed female and pupal exuviae, 28.vii.91 KS14 Pe36Im, Lake H, Esayoo Bay, Borup, Ellesmere Island, leg. K. Silvester. Paratypes: Pharate adult female, 13.vii.91 KS9 P2, Lake H, Esayoo Bay, Borup, Ellesmere Island, leg. K. Silvester; Pupal exuviae, 18.vii.91 KS4 Pe107, Lake B, Midnight Sun Valley, Borup, Ellesmere Island, leg. K. Silvester; 18.vii.91 KS4 Pe62, Lake B, Midnight Sun Valley, Borup, Ellesmere Island, leg. K. Silvester (CNC).

Paratypes: Lake A, Midnight Sun Valley, Borup, Ellesmere Island 20.vii.91 2 partly eclosed females + pupal exuviae, 2 pupal exuviae; Lake B, Midnight Sun Valley, Borup, Ellesmere Island, 18.vii.91: 10 pupal exuviae. Lake H, Esayoo Bay,Borup, Ellesmere Island, 8.vii.91, 13.vii.91, 16.vii.91, 22.vii.91, 25.vii.91, 28.vii.91: 1 partly eclosed female + pupal exuviae; 2 pharate adults; 25 pupal exuviae; leg. K. Silvester, coll. PHL.

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Dr. Kazimierz PATALAS
Department of Fisheries and Oceans
Freshwater Institute
501 University Crescent
Winnipeg,Manitoba Canada
R3T 2N6

January 11. 1994

Lieutenant Henry Parker

MARKHUSET Gambles
Gambles Lane
Woodsman Cote
CHELTENHAM (England)
GL52 4PU

Dear Lieutenant,

Please find enclosed the results of the analysis of the plankton samples from Ellesmere Island as well as some reprints of my paper on zooplankton.
As I mentioned to you in our last telephone conversation, I have retired year ago but I am still continuing my plankton works on geographical distribution of crustaceans in Canada.

I wish you all the best in this New Year and in all the following years.

Cordially yours

The results of the analysis of the samples from Ellesmere Island
Midnight Sun Valley (80° 50' N 81° 00 W) June - Aug. 1991
The following species were found in the provided samples from
Henry's Lake, Lake A, Lake B and Lake C. :

Daphnia middendorffiana Fischer
Bosmina longirostris (O.F.Mueller)
Chydorus sphaericus (O.F.Mueller)
Cyclops scutifer Sars
Eucyclops agilis (Koch)
Macrocyclops magnus Marsh
Limnocalanus macrurus Marsh

HENRY'S Lake

Date	Daphnia middend.	Bosmina longir.	Chydorus sphaer.	Cyclops scutifer	Eucycl. agilis	Macroc. magnus	Limnoc macrur
8.7.91					X		X
12.7.91							
B/15/15Vx3							X
B/15/8 Vx6			X		X		X
22.7.91							
A/8/7.5Vx1							X
A/8/4Vx2							X
B/15/15Vx1							X
B/15/8Vx2							X
C/6.5/6.5Vx1							X
C/6.5/3.5Vx2							X
28.7.91							
A/8.5/8Vx1							X
B/15.5/15Vx1							X
C/8.5/8Vx1							X
07.8.91							
A/8.5/8Vx1							X
A/8.5/4Vx2							X
B/15.5/15.5Vx1							X
C/8.5/8Vx1							X
C/8.5/4Vx2							X